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COMPARATIVE REVISION OF *SCOMBEROIDES*, *OLIGOPLITES*, *PARONA*, AND *HYPACANTHUS* WITH COMMENTS ON THE PHYLOGENETIC POSITION OF *CAMPOGRAMMA* (PISCES: CARANGIDAE)[1]

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INTRODUCTION

This study evolved as a result of our efforts to unscramble the confused synonymies of Indo-Pacific carangids of the genus *Scomberoides*. The initial effort led us to review the species of *Oligoplites*, a New World genus closely related to *Scomberoides*, last treated by Schultz (1945). It soon became obvious that our paper would not be complete unless we included coverage of several monotypic Atlantic genera that are superficially similar to the 'leatherjackets' of American waters. Comparison of these three carangid genera is especially desirable because they, together with *Oligoplites*, are the only ones, of the 18 Atlantic genera that we currently recognize, which do not occur on both sides of the Atlantic. The combinations of characters exhibited by these genera have impressed us with the artificiality of the present subfamilial partitioning of the Carangidae. In discussing relationships of these genera it is necessary to emphasize some of the inadequacies of the present subfamilial classification of the Carangidae.

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Special thanks are due J. R. Paxton and R. J. McKay for providing identifications and locality data for collections of *Scomberoides* housed in their respective institutions, thus confirming our tentative zoogeographical conclusions. Tomio Iwamoto examined MNHN types of *Scomberoides* (subsequently re-examined by us) that provided much of the impetus for initiation of the present paper.

Additional help came from various sources. James E. Böhlke and William N. Eschmeyer facilitated our study by making literature available. Phillip C. Heemstra called to our attention several pertinent references. William H. Hulet and Francisco J. Palacio assisted in translating Italian and Portuguese literature. Grady W. Reinert illustrated the specimens shown in figure 1. The manuscript was typed by Mrs. Kathie Jeffries.

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Frederick H. Berry and C. Richard Robins reviewed the manuscript and offered suggestions for improvement.

Major collections of *Scomberoides* critical to our study were obtained in Ceylon under Smithsonian Foreign Currency Grant 3818, C. Richard Robins and Frederick H. Berry, principal investigators. Field work in Ceylon was greatly facilitated by the cooperation of Mr. A. S. Mendis, Deputy Director (Research), Department of Fisheries, Ceylon. The second author was able to pursue this study through support of the National Geographic Society-University of Miami Deep-Sea Biology Program (University of Miami research account 8852R), Gilbert L. Voss, Principal Investigator. Partial support was also provided by a grant from the Tai Ping Foundation to Smith-Vaniz for study of Indian Ocean Carangidae.

CHARACTERS AND METHODS

Osteological terminology generally follows that of Suzuki (1962); a specific exception is the "postmaxillary process" which is here more appropriately termed a premaxillary spur since it is a posterior projection on the premaxilla that braces the maxilla. A basibranchial is defined (Nelson, 1969, p. 480) as the median part of the gill arch endoskeleton that lies between successively paired arch-elements. The number of the basibranchial refers to the paired arch-element behind it.

Rayless predorsal interneurals are termed predorsal bones (Smith and Bailey, 1961). All carangids have at least 3 predorsal bones; counting posteriorly, the fourth element, whether supporting a dorsal-fin spine or not, has a well developed spinelike projection on its anterodorsal margin. This structure, commonly termed a procumbent spine, may occasionally protrude through the skin. In the genera treated in this study, all anterior dorsal pterygiophores support a single fin spine. Thus, a shortening of the dorsal-fin base through loss of anterior spines results in a concomitant increase in number of predorsal bones. The first fin-ray (spine) is often greatly reduced, depressed posteriorly, and can easily be overlooked. In carangids there is a tendency for the number of external spines to decrease in large specimens due to absorption, as evidenced from examination of radiographs. In this study large specimens were not x-rayed or dissected; thus the frequency of specimens with the least number of dorsal spines may be slightly lower than indicated in tables 2 and 4.

The last dorsal- and anal-fin rays are split to the base, have a single pterygiophore, and were counted as one ray.

The first caudal vertebra has a well developed haemal spine which articulates with the first anal pterygiophore; the urostyle is regarded as the terminal caudal vertebra.

Counts of outer row dentary teeth in *Scomberoides* and *Oligoplites* are lateral counts (one side only). Counts were made on the dentary that appeared to have the most teeth. Broken teeth were counted but empty tooth sockets and teeth that had not attained a functional position in the outer row were excluded. Symphyseal dentary canines were also excluded in the case of *Scomberoides*.

Pectoral-fin ray counts are lateral counts (one side only). The dorsalmost fin-ray element is spinelike and was counted separately.

Gillraker counts are lateral counts and were usually made on the right side of each fish. Only gillrakers on the lateral side of the first arch were counted. The gillraker at the angle of the upper and lower limb has the major portion of its base on the ceratobranchial bone and was included in the count of the lower limb. Rudimentary gillrakers (with the width of raker greater than its length) were not included in the counts.

All measurements are straight line (point to point) measurements. Measurements smaller than 120 mm. were made with dial calipers. Measurements given in the material examined sections are fork length (FL), unless otherwise stated, and have been rounded off to the nearest millimeter. In large fishes with relatively rigid caudal fins, such as carangids, the end of the hypural plate is often difficult to determine precisely. In addition to being easier to determine than standard length, fork length is more familiar to fishery biologists, who should have the greatest need to identify carangids. The following measurements were used in this study:

Fork length (FL). Snout tip to tip of shortest median caudal-fin ray.
Standard length (SL). Snout tip to posterior end of hypural bones (caudal base).
Head length (HL). Snout tip to posterior margin of fleshy opercular flap.
Snout-postorbit length. Snout tip to anterior margin of posterior adipose eyelid.

Snout length. Snout tip to posterior margin of anterior adipose eyelid.
Upper jaw length. Snout tip to posterior margin of maxilla.
Body depth D_2 to A_2. Origin of terminal dorsal spine to origin of terminal anal spine.
Height of fin lobes. Origin of fin to tip of longest segmented ray.
Pectoral-fin length. Origin of spine to tip of longest ray.

Abbreviations of institutions cited are as follows:

AMNH	American Museum of Natural History, New York City
AMS	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
FMNH	Field Museum of Natural History, Chicago
MNHN	Muséum National d'Histoire Naturelle, Paris
NFIS	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt
SIO	Scripps Institution of Oceanography, University of California, La Jolla
SU	Stanford University, Division of Systematic Biology (collection transferred to CAS)
TABL	Southeast Fisheries Research Center, National Marine Fishery Service, Miami (formerly Tropical Atlantic Biological Laboratory)
UCLA	University of California at Los Angeles
UMML	University of Miami, Rosenstiel School of Marine and Atmospheric Science, Miami
USNM	National Museum of Natural History, Division of Fishes, Washington, D. C.
ZMC	Zoological Museum, Copenhagen
WAM	Western Australian Museum, Perth.

Uncataloged California Academy of Sciences specimens collected under the auspices of the George Vanderbilt Foundation (GVF) are reported under their register or station numbers. Most collections from Ceylon are uncataloged and listed by station numbers. Abbreviations refer to the following collectors listed in chronological order of their visits to Ceylon: F. J. Schwartz; W. F. Smith-Vaniz; P. C. Heemstra; C. C. Koenig.

Localities in material examined sections are abbreviated. Summary statements of material examined include only specimens examined by the authors.

Scomberoides Lacépède, 1802

Scomberoides Lacépède, 1802, p. 50 (type-species: *Scomberoides commersonianus* Lacépède, 1802, by subsequent designation of Jordan, 1917, p. 60).

Orcynus Rafinesque, 1815, p. 84 (*nomen nudum*; substitute name for *Scomberoides* Lacépède, 1802).

Chorinemus Cuvier *in* Cuvier and Valenciennes, 1831, p. 367 (type-species: *Scomberoides commersonianus* Lacépède, 1802, by subsequent designation of Jordan, 1917, p. 137).

Rhaphiolepis Fowler, 1905, p. 59 (as a subgenus of *Scomberoides*; type-species: *Chorinemus tol* Cuvier *in* Cuvier and Valenciennes, 1831, by original designation).

Eleria Jordan and Seale, 1905, p. 774 (type-species: *Elcria philippina* Jordan and Seale, 1905 = *Chorinemus tala* Cuvier *in* Cuvier and Valenciennes, 1831, by monotypy).

Palaeoscomber Smirnov, 1936, p. 49–59 (type-species: *Palaeoscomber spinosus* Smirnov, 1936, by original designation).

The carangid genus *Scomberoides* comprises four recent and one fossil species of tropical and subtropical marine fishes restricted to the Indian and western and central Pacific oceans. All recent species attain at least 45 cm. fork length. *Scomberoides commersonianus*, the largest species, occasionally exceeds 100 cm. and is a valued game fish. In some areas *S. commersonianus* supports a seasonal fishery of considerable importance. Major catches are obtained from drift nets set at depths of 15 to 18 m. in waters surrounding offshore islands (James, 1967). Depending on the region, scomberoides are considered excellent food fishes (Smith, 1949, p. 224) or they are mostly salted and not generally esteemed (Chan, 1968, p. 82).

Halstead *et al.* (1972) give a detailed description of the venom apparatus of *Scomberoides lysan*. Venom glands are associated with the first seven dorsal-fin spines and the first two anal spines. The anal spines, rather than the dorsal spines, are the most venomous. The anal spines are equipped with a frictional locking device which resembles that found in the fin spines of catfishes and balistid triggerfishes. *Scomberoides lysan* is capable of inflicting painful stings. The nearly identical morphology of these spines in the other species of *Scomberoides* and *Oligoplites* (see comments under *O. saurus*) suggest that all species of both genera are venomous.

The osteology of *Scomberoides* has received inadequate attention. The only species studied in detail (under the name *Chorinemus orientalis*) is *Scomberoides lysan* (Suzuki, 1962). The only known fossil species of *Scomberoides* was originally described as belonging to a new genus, *Palaeoscomber*, of Scombridae (Smirnov, 1936) and was subsequently redescribed as a species of *Oligoplites* (Danil'chenko, 1960).

The nomenclature of *Scomberoides* species has been greatly confused by a plethora of nominal species inadequately described by early workers. Differences ascribed to nominal species have frequently been based on unrecognized ontogenetic changes. Changes in dentition associated with growth led Jordan

Table 1. *Nominal species of* Scomberoides *recognized in selected publications with our present allocation.*

Authors	Species			
Present Study	*commersonianus*	*tala*	*lysan*	*tol*
Smith (1970)	*lysan*	—	*tolooparah*	*tala*
Williams (1958)	*lysan*	—	*sanctipetri*	—
Roxas and Agco (1941)	*lysan*	*tala*	*tolooparah*	*tol*
Weber and De Beaufort (1931)	*lysan*	*tala*	*tolooparah* *sanctipetri*	*tol*
Wakiya (1924)	*lysan*	—	*sanctipetri* *orientalis* *moadetta*	*formosanus*
Day (1878)	*lysan*	*tala* *toloo*	*sanctipetri*	*moadetta*

and Seale (1905, p. 774) to describe a new genus and species based on juveniles of *S. tala.* The failure of recent workers to critically read original descriptions and examine types adequately has resulted in the consistent misapplication of the name *Scomberoides lysan* (Forskål). Because of the confused nomenclature of *Scomberoides* species, we present in table 1 a list of the species recognized in several major papers with our present allocation of them. An annotated list of the nominal species of *Scomberoides* and *Oligoplites* is given in the appendix.

Nomenclature. Considerable confusion exists as to whether *Scomberoides* Lacépède, 1802 was validly described and thereby has priority over *Chorinemus* Cuvier, 1831. Williams (1958) briefly discussed the problem and rejected *Scomberoides,* as did Weber and De Beaufort (1931) and Smith (1970). Rejection of *Scomberoides* as a valid generic name by several recent workers is probably attributable to the comments of Barnard (1927, p. 562) who credits the rejected name to Lacépède (1800), in which only a figure is given with the caption "Scomberoide commersonnien." Jordan (1917, p. 60) rightly credits *Scomberoides* to Lacépède (1802), in which "Les Scomberoides" was latinized to accommodate the description of three new species. *Caranx* and *Trachinotus,* widely accepted carangid generic names, originate from the same work and were described in the same manner as *Scomberoides.*

Williams (1958, p. 416) states that "the use of *Chorinemus* has been common and widespread since 1833 whilst *Scomberoides* has been restricted (except Wakiya, 1924) to American authors of the last 75 years." He further states "should *Scomberoides* be proved to have priority over *Chorinemus* C. V. . . . . , then a case exists for submission to the International Commission of Zoological Nomenclature for a suspension of the Rules, in that strict application of the Rules will clearly result in greater confusion than uniformity." In their review of the Philippine Carangidae Roxas and Agco (1941) used *Scomberoides* as did Oshima (1925) and McCulloch (1929). Except for Rofen (1963), American authors of the last 75 years, the most recent of which are Gosline and Brock (1965), have consistently used *Scomberoides* instead of *Chorinemus*. Although Williams apparently attaches little importance to this, it should be noted that American authors are responsible for a large portion of the literature treating these fishes.

Confusion also exists as to what constitutes the type-species of the genus. Several workers have recognized *Scomberoides noelii* as the type-species. Lacépède (1802) described three species in his new genus, listing them on page 50 with brief diagnoses (descriptions expanded on following pages) in the following order: (1) *Scomberoides noelii*; (2) *S. commersonianus*; (3) *S. saltator*. He did not, however, specifically designate a type-species. The first author to subsequently designate a type-species for *Scomberoides* in accordance with Article 69a of the International Code of Zoological Nomenclature was Jordan (1917, p. 60), who selected *S. commersonianus*. The published illustration of *S. commersonianus* (as "Scomberoide commersonnien") (Lacépède, 1800 pl. 20, Fig. 3) is sufficiently accurate for positive identification.

The possession of needlelike scales does distinguish the type-species of *Rhaphiolepis* from its congeners. However, the transition from oval-shaped to needlelike scales is obvious in *Scomberoides* (see figure 3), and we do not believe that recognition of subgenera in such a small group of closely related species is justified. The sole character mentioned in the original description to distinguish *Eleria* from *Scomberoides* was based on unrecognized ontogenetic changes in dentition (see discussion under *S. tala*). Reasons for referral of *Palaeoscomber* to the synonymy of *Scomberoides* are discussed under *S. spinosus*.

Description. Body moderately to strongly compressed. Adipose eyelids moderately to poorly developed. Body, except head, covered with embedded scales, broadly lanceolate to needlelike. Lateral-line scales not developed into scutes. Lateral line without side branches, straight except for slight curve over pectoral fin. Anterior rim of shoulder girdle smooth, without fleshy papillae or deep groove near isthmus. Premaxillae not protractile, connected anteriorly to snout at midline by a wide fleshy bridge. Swimbladder strongly bifid posteriorly, length of bifurcated portion of swimbladder equal to or greater than undivided part. Posterior dorsal- and anal-fin rays consisting of semidetached finlets, distal fourth to half of ray not connected by interradial membrane (unattached portion of rays increasing with growth); ultimate and penultimate rays more closely spaced than adjoining rays, fully connected by interradial membrane; none of dorsal- or anal-fin rays produced into long filaments. Pelvic fins relatively short, depressible into shallow abdominal grooves. Pectoral fins short, not falcate, 53 to 71 percent head length in adults. Maxilla extends posteriorly from middle of eye to well behind orbital rim, 43 to 65 percent head length, in adults.

Predorsal bones 3, rarely 4 (4 in one of 60 specimens); dorsal-fin rays VI or VII + I, 19–21; total dorsal-fin rays 27–29. Anal-fin rays II + I, 16–20. Pectoral-fin rays I, 16–18. Pelvic-fin rays I, 5. Vertebrae 10 + 16 = 26; epipleural ribs 9 or 10. Branchiostegal rays 3 + 5 (epihyal + ceratohyal). Upper gillrakers 0–8; lower gillrakers 7–20; total gillrakers 8–27.

Fronto-supraoccipital crest low; temporal crest extending forward to edge of cranium slightly in front of middle of orbit; preorbital region short. Epiotics broadly united along midline of cranium internally. Zygapophyses of exoccipital joined beneath foramen magnum. Parasphenoid not expanded into a broad, flattened plate posteriorly. Myodome with broad, posterior opening. Basioccipital without a pair of lateral processes on ventral surface. Ascending process of premaxilla short and triangular; maxilla long and slender, rather closely attached to premaxilla. Premaxillary spur absent. Small supramaxilla present. Interosseous space between dorsal arm of dentary and upper margin of articular greatly reduced. Well developed teeth on dentary, premaxilla, palatine, and vomer; two distinct rows of dentary teeth (see discussion under Zoogeography and Relationships Section); symphyseal premaxillary and dentary teeth of juveniles (except *S. lysan*) robust and caniniform. Mesopterygoids covered with firmly ankylosed, minute, granular teeth. Pharyngeals not noticeably enlarged, covered with sharp, pointed teeth.

Well developed suborbital shelf present; lower and posterior suborbitals not greatly expanded posteriorly. Basibranchials 1–2 with a pair of tooth plates, third basibranchial with two or more irregular tooth plates. Lower limb of posttemporal not noticeably short or thickened. Postcoracoid process absent. Interpelvic keel well developed; post pelvic process of each side coalesced entire length, not forming an apical fork. Inferior vertebral foramina absent. First anal pterygiophore and haemal spine of first caudal vertebra firmly attached to form a strong strut. Anal pterygiophore expanded anterolaterally to form roof over first two anal spines; first two anal spines articulated proximally with each other; second anal spine asymmetrical, with deep groove on one side of anterior face. Caudal skeleton with 2 epurals and 2 pairs of uroneurals.

Key to Recent Species of *Scomberoides*

Color pattern will readily separate most specimens of the four species. In large individuals and especially in small specimens that are not freshly caught the spots may fade or completely disappear; this is particularly true of fish market specimens.

1a. Gillrakers 8 to 15; dorsal-fin lobe uniformly pigmented 2
1b. Gillrakers 21 to 27; distal half of dorsal-fin lobe abruptly and heavily pigmented 3
2a. Large oval blotches above or touching lateral line; upper jaw extends well beyond posterior margin of eye, especially in adults (fig. 2a); snout 21 to 26 (mean 23.4)

percent HL; dentary teeth of inner and outer rows subequal in adults; specimen figure 1a .... *S. commersonianus*

2b. Vertically elongate blotches intersecting lateral line; upper jaw extends slightly beyond posterior margin of eye (fig. 2b); snout 26 to 30 (mean 28.2) percent HL; inner row dentary teeth distinctly larger than outer row teeth in adults; specimen figure 1b .... *S. tala*

3a. Double series of 6 to 8 dusky, roundish blotches above and below lateral line, occasionally connected by narrow isthmus; scales lanceolate (fig. 3b); specimen figure 1c .... *S. lysan*

3b. Oval or vertically oblong blotches, the first 4 or 5 intersecting lateral line; scales slender, needlelike (fig. 3d); specimen figure 1d .... *S. tol*

Scomberoides commersonianus Lacépède.

(Figures 1a, 2a, 3a, 4a, 5–7, 14c, 16b, 19, 23b, 25b; tables 2–3.)

Scomberoides commersonianus Lacépède, 1802, p. 50 (type locality Madagascar).
Scomber madagascariensis Shaw, 1803, p. 590, pl. 85 (type locality Madagascar).
Chorinemus exoletus Ehrenberg *in* Cuvier and Valenciennes, 1831, p. 379 (278) (based solely on an unpublished drawing by Ehrenberg of a fish from Lohaia, Red Sea).
Chorinemus delicatulus Richardson, 1846, p. 269 (based solely on a drawing in the Reeves Collection of Chinese fish drawings).
Chorinemus leucopthalmus Richardson, 1846, p. 269 (based solely on a drawing in the Reeves Collection of Chinese fish drawings).

Nomenclature. The figure of *S. commersonianus* (as "Scombéroide commersonnien") and original description are sufficiently accurate for positive identification, and the name has consistently been applied to the correct species, although usually in synonymy (see nomenclature section under *S. lysan*). Although in the original description *S. commersonianus* was spelled with a double "n," we prefer the emended spelling with a single "n," which is correct.

The description of *Chorinemus exoletus* refers to a deep-bodied species with a long upper jaw. This together with the stated type locality is sufficient to confidently identify it as conspecific with *S. commersonianus.*

Whitehead (1969) has published the original drawings upon which the descriptions of *Chorinemus delicatulus* and *C. leucopthalmus* are based. These drawings and that of *Scomber madagascariensis* are reasonably diagnostic and are undoubtedly based on *S. commersonianus.* Although the large oval blotches characteristic of *S. commersonianus* are not shown on the sides of *Chorinemus delicatulus* and *C. leucopthalmus,* they rapidly fade and disappear in dead specimens.

Description. Characters given in the generic description are not repeated here. Frequency distributions of selected meristic characters are given in table 2. Dorsal-fin rays VI-VII + I, 19–21; anal-fin rays II + I, 16–19; pectoral-fin rays, I, 17–19. Gillrakers 0–3 + 7–12 = 8–15. Upper jaw extending well beyond posterior margin of eye, especially in adults (fig. 2a). Scales broadly lanceolate (fig. 3a). Inner and outer row of dentary teeth subequal in adults (fig. 4a); dentary typically with one or two pair of symphyseal canines, at least

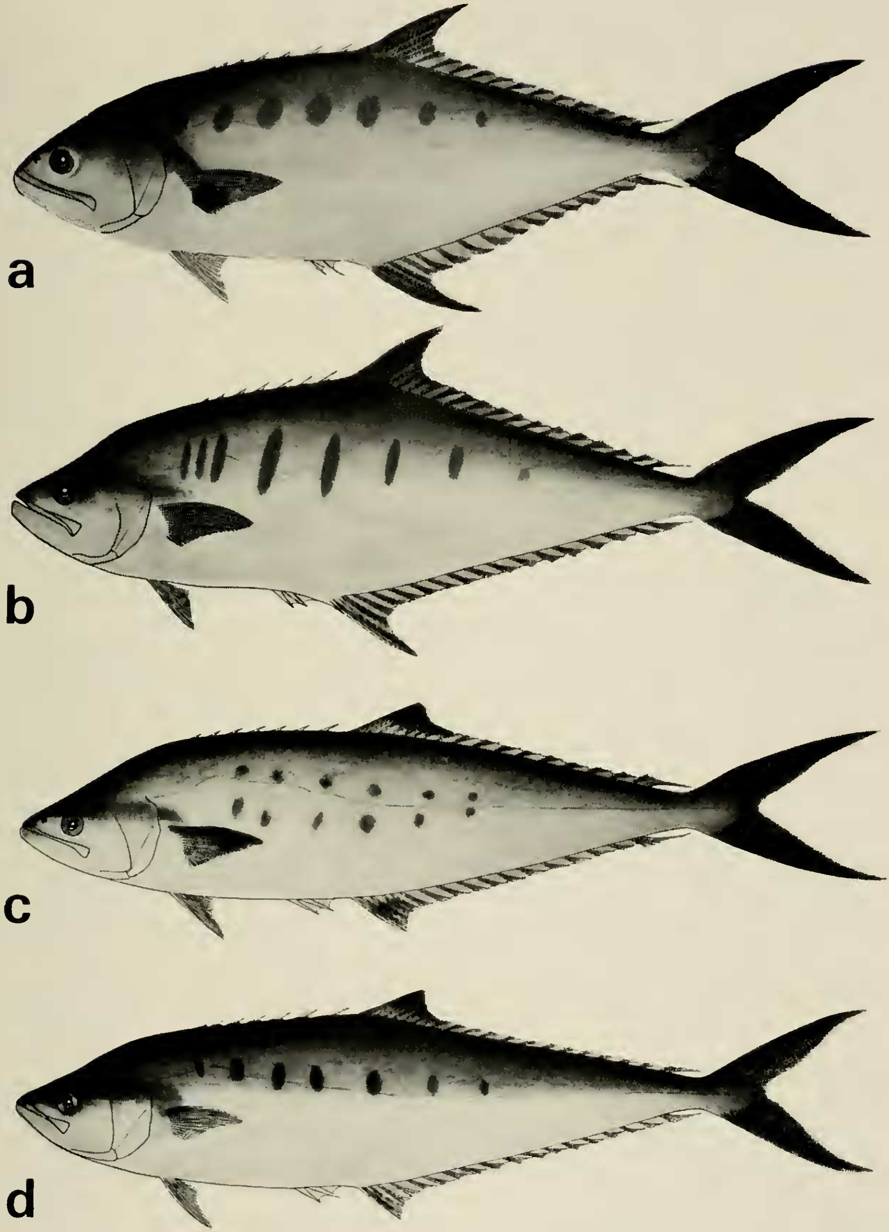

Figure 1. *Scomberoides* species: a, *S. commersonianus*, TABL 107366, 468 mm. FL; b, *S. tala*, TABL 107365, 464 mm. FL; c, *S. lysan*, TABL 107364, 523 mm. FL; d, *S. tol*, TABL 107363, 450 mm. FL.

Table 2. *Frequency distribution of meristic characters in* Scomberoides *species.*

	Dorsal-Fin Rays							Anal-Fin Rays						
	D_1 Spines		Segmented Rays					Segmented Rays						
Species	VI	VII	19	20	21	N	$\bar{x}$	16	17	18	19	20	N	$\bar{x}$
commersonianus	4	83	23	63	1	87	19.7	2	13	71	3	—	89	17.8
tala	6	84	11	73	6	90	19.9	—	3	80	6	—	89	18.0
lysan	8	86	3	83	8	94	20.0	—	5	83	7	—	95	18.0
tol	2	89	1	44	46	91	20.5	—	—	22	68	2	92	18.8

	Upper Gill Rakers											Lower Gill Rakers															
Species	0	1	2	3	4	5	6	7	8	N	$\bar{x}$	7	8	9	10	11	12	13	14	15	16	17	18	19	20	N	$\bar{x}$
commersonianus	10	30	31	18	—	—	—	—	—	89	1.6	1	10	26	36	15	1	—	—	—	—	—	—	—	—	89	9.6
tala	—	2	66	20	—	—	—	—	—	88	2.2	1	24	55	6	2	—	—	—	—	—	—	—	—	—	88	8.8
lysan	—	—	—	1	2	21	44	22	6	96	6.1	—	—	—	—	—	—	—	—	1	2	26	45	18	2	96	17.5
tol	—	—	—	—	1	24	55	11	—	91	5.6	—	—	—	—	—	—	—	—	—	—	12	31	41	7	91	18.5

	Total Gill Rakers																					
Species	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	N	$\bar{x}$
commersonianus	3	11	18	18	17	10	11	1	—	—	—	—	—	—	—	—	—	—	—	—	89	11.3
tala	—	—	—	1	20	46	18	3	—	—	—	—	—	—	—	—	—	—	—	—	88	12.0
lysan	—	—	—	—	—	—	—	—	—	—	—	—	—	3	14	22	29	12	11	5	96	23.9
tol	—	—	—	—	—	—	—	—	—	—	—	—	—	1	4	13	35	26	12	—	91	24.3

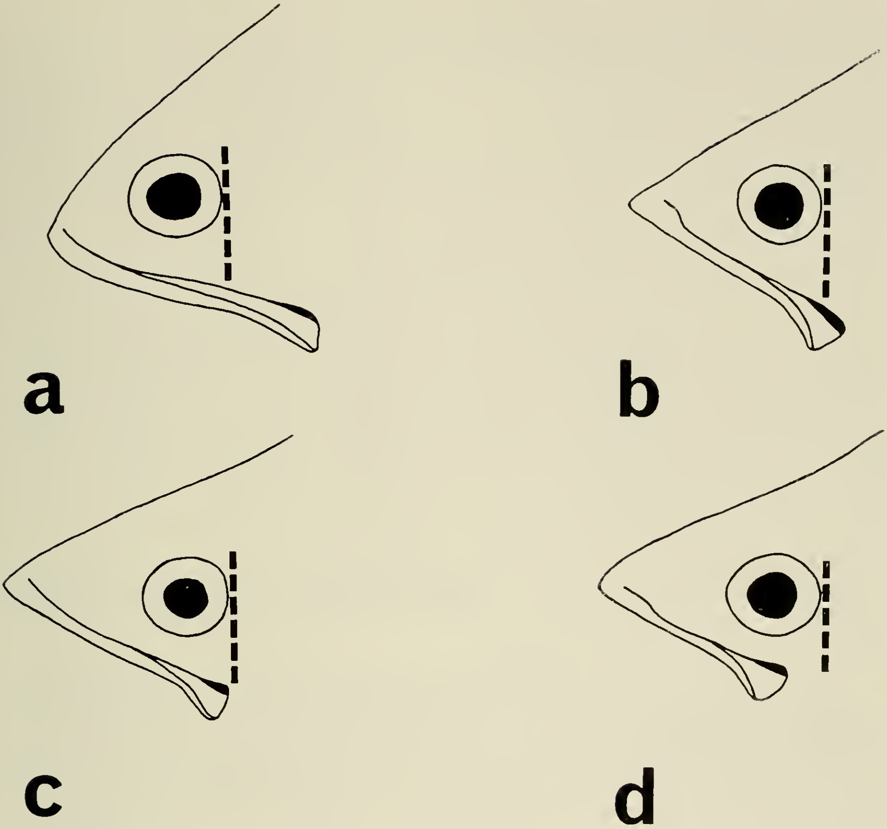

Figure 2. Upper jaw development of adult *Scomberoides* species: a, *S. commersonianus*, TABL 107192, 355 mm. FL; b, *S. tala*, TABL 107712, 351 mm. FL; c, *S. lysan*, TABL 107364, 412 mm. FL; d, *S. tol*, TABL 107714, 410 mm. FL. Maxilla shown in black.

in young; young with dentary teeth of outer row numerous and considerably more closely spaced than inner row teeth.

Proportional measurements apply only to specimens longer than 150 mm. FL, and are expressed as percent FL unless otherwise stated. Depth (origin D_2 to A_2) 25.7–36.2; height dorsal-fin lobe 14.4–19.8; height anal-fin lobe 13.5–18.5; upper jaw 55.9–64.6 percent head length; snout 20.6–26.0 percent head length.

Pigmentation. Sides with 5 to 8 large oval blotches above or touching lateral line, first two may intersect lateral line. Dorsal and anal fins uniformly pigmented. Pectoral fin of adults frequently with a dusky blotch ventrally. In life, body gray to silvery white ventrally, dusky green or bluish dorsally;

Table 3. *Comparison of several proportional measurements in* Scomberoides *species expressed as hundredths of head length.*

Species	<20 cm. Range FL	N	Upper Jaw Length		Snout Length	
			Range	$\bar{x}$	Range	$\bar{x}$
commersonianus	82–198	19	59–64	60.1	21–26	23.6
tala	71–199	23	53–61	58.2	26–30	28.3
lysan	45–189	20	51–56	53.9	28–31	29.0
tol	44–181	17	47–51	48.6	30–33	31.3

Species	>20 cm. Range FL	N	Upper Jaw Length		Snout Length	
			Range	$\bar{x}$	Range	$\bar{x}$
commersonianus	224–943	64	56–65	60.6	21–26	23.4
tala	201–571	58	54–61	57.8	26–30	28.2
lysan	201–585	65	50–54	51.6	28–32	30.0
tol	209–468	70	43–49	46.3	29–33	31.3

lateral blotches plumbeous gray. Large individuals often golden, especially ventrally. Annunziata and Cedrone (1972, p. 61) present a color photograph of a large specimen from Madagascar.

Distribution. Widely distributed throughout the Indian Ocean and Indo-Australian Archipelago. The species has also been reliably reported from the Red Sea and Persian Gulf. *Scomberoides commersonianus* appears to be restricted to neritic waters and does not occur east of the New Guinea-Solomon Islands region. Records of the species (as *S. lysan*) from Tahiti and other central Pacific islands are based on misidentifications.

Material (96 specimens, 82–943 mm. FL, from 53 collections). KENYA: Mombasa Fish Market, TABL uncataloged *Anton Bruun* cruise 9 station, FT-2 (1: 398). WEST PAKISTAN: off Karachi, TABL uncataloged (3: 236–295). INDIA: Gulf of Kutch, TABL uncataloged (1: 203); Bombay, TABL 107190 (1: 384), 107350 (1: 158); Palk Strait, TABL 107292 (4: 127–288), TABL uncataloged FHB 66–36 (1: 766); Porto Novo, TABL 107303 (1: 198), TABL uncataloged (1: 190). CEYLON: TABL 107192 FJS 69–41 (9: 327–422), FJS 69–45 (6: 195–244), FJS 69–64 (1: 474), FJS 69–50 (1: 400), TABL 107366 S-V 69–77 (3: 303–476), S-V 69–86 (2: 224–254), S-V 69–126 (1: 335), S-V 69–151 (2: 754–762), PCH 69–183 (1: 617), PCH 69–185 (7: 123–158), TABL 107715 PCH 69–201 (3: 398–443), PCH 69–218 (10: 130–168), PCH 69–267 (1: 503), PCH 69–305 (1: 913), CCK 69–1 (1: 843), CCK 69–44 (1: 797), CCK 69–53 (1: 475), CCK 69–60 (7: 234–349), CCK 69–97 (2: 160–218). GULF OF THAILAND: GVF station 57–45 (2: 355–391), GVF station 57–92 (1: 520), GVF station 57–83 (2: 559–579), GVF station 60–113 (2:

849–943), GVF station 60–146 (2: 727–729), GVF-1548 (1: 133), GVF-1557 (2: 186–197), GVF-2195 (1: 93, cleared and stained), GVF-2513 (2: 727–739), GVF-2546 (1: 291), GVF-2547 (6: 243–612). HONG KONG: GVF station HK-111 (1: 829). PHILIPPINES: Luzon, USNM 72190 (1: 172), 83447 (1: 241), 168322 (1: 309), SU 20341 (2: 82–116); Samar, USNM 149810 (1: 129); Iloilo, USNM 72189 (1: 129), 149812 (1: 152); Palawan, USNM 149813 (1: 128), 149815 (1: 151). NORTH BORNEO: Sandakan, USNM 149814 (1: 172), 168323 (1: 234). JAVA: Djakarta, TABL 107300 (1: 266). AUSTRALIA: Western Australia, Exmouth Gulf, Onslow, WAM P.2772 (1: 302), P.15487 (1: 175); Port Hedland, WAM P.180 (1: 329); Broome, WAM P.555 (1: 95); Northern Territory, Charles Point, AMS IA.7781 (1: 164); Port Darwin, AMS I.9778 (1: 300), IA.4375 (1: 280); Darwin, AMS IB.3168 (1: 420), IB.3171 (1: 85); Bedwell Point, AMS IA.7678 (1: 356); Gulf of Carpentaria, Groote Eylandt, USNM 173954 (4 of 7: 240–345); 17°22'S., 149°45'E., AMS I.15557–118 (5: 87–172); Queensland, Burdekin River, USNM 47835 (1: 275), AMS A.18299–300 (2: 285–615); Lindeman Island, AMS IA.6279 (1: 297); Hayman Island, AMS IA.6104 (1: 460); New South Wales, Port Jackson, USNM 47910 (1: 357). NEW GUINEA: AMS A.12694 (1: 300); Port Moresby, AMS I.13357 (1: 565).

Scomberoides tala (Cuvier).

(Figures 1b, 2b, 3c, 4b, 5–7, 15b, 17, 19, 24b; tables 2–3.)

Chorinemus tala Cuvier *in* Cuvier and Valenciennes, 1831, p. 377 (type locality Malabar).

?*Chorinemus toloo* Cuvier *in* Cuvier and Valenciennes, 1831, p. 377 (description based on "toloo parah" Russell, 1803, p. 29, pl. 137, Vizagapatam).

Eleria philippina Jordan and Seale, 1905, p. 744, fig. 1 (type locality Negros Island, Philippines).

Chorinemus hainanensis Chu and Cheng, 1958, p. 317, fig. 2 (type localities Sanya, Kanchium, Kwonghoi, and Chinglan, China).

Nomenclature. In the Muséum National d'Histoire Naturelle there are two collections (A. 6587 and A. 6588) from Malabar, collected by Belanger, which are labeled syntypes of *Chorinemus tala* Cuvier. A. 6588, here designated lectotype of *C. tala*, is a single specimen 298 mm. SL. A. 6587 consists of two specimens of *S. tol* Cuvier. In his treatment of the western Indian Ocean species of *Scomberoides*, Smith (1970, p. 221) referred *S. tol* to the synonymy of *S. tala*. This erroneous action was based on his examination of one of the specimens of A.6587. Smith apparently was unaware of the existence of other material labeled as types of *S. tala*, and fortunately did not designate a lectotype.

Although Weber and De Beaufort (1931, p. 282) and Smith (1970, p. 219) considered the species insufficiently described for positive identification, the following statements given in the original description of *Chorinemus tala* leave no doubt as to its specific identity: (1) "*Chorinemus tala* differs [from the

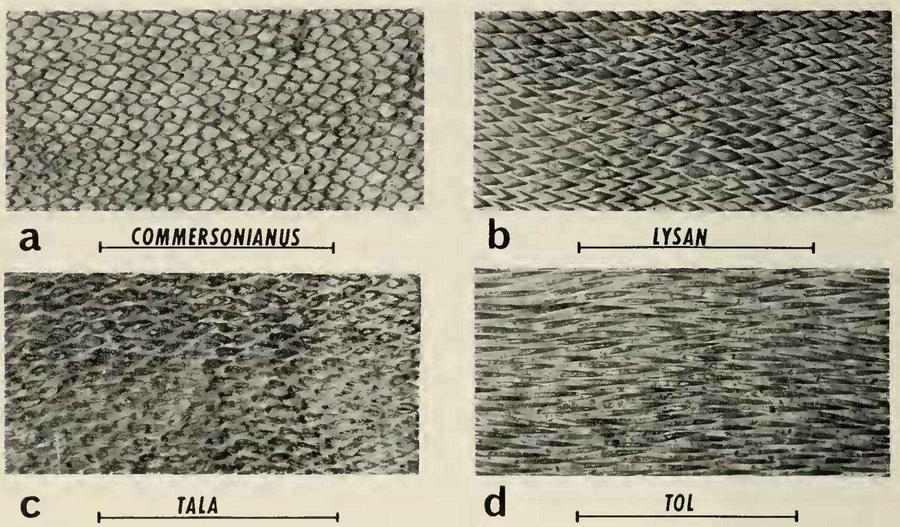

FIGURE 3. Scales of *Scomberoides* species (from area between anal-fin origin and lateral line): a, *S. commersonianus*, TABL 107715, 398 mm. FL; b, *S. lysan*, TABL 107364, 412 mm. FL; c, *S. tala*, TABL 107712, 370 mm. FL; d, *S. tol*, TABL 107714, 410 mm. FL. Scale, 20.0 mm.

preceding species, *C. commersonianus*] by a smaller gape, a maxillary that hardly extends beyond the posterior border of the orbit. (2) The maxillary is, in addition, covered by the suborbital and only shows its posterior third; it is enlarged more posteriorly and is cut off more squarely. (3) The teeth are stronger in proportion. (4) The curve of the snout is a little less straight . . . , but the shape of the body, the scales, the lateral line and the number of rays are as in the preceding species."

Statement 4 and the fact that *S. tala* was compared with *S. commersonianus*, suggest that the name *S. tala* applies to a deep-bodied species with high fin lobes. *Scomberoides tol* and *S. lysan* are both relatively slender species (fig. 6) and have shorter fin lobes (fig. 7) than do the other two species of *Scomberoides*. Statements 1 and 4 exclude *S. tol*, in which the maxilla does not reach the posterior border of the orbit and the scales are needle-shaped (fig. 3d). Statement 3 excludes *S. lysan* and *S. tol*, in which the teeth in both jaws are relatively small in adults and applies best to the species here recognized as *S. tala*, which has the largest teeth (fig. 4b). Statements 1 and 2 are sufficient to exclude *S. commersonianus* (compare figs. 2a and 2b).

The fact that Cuvier recognized *S. commersonianus* (and several of its synonyms) and described as new, from Malabar specimens, examples of the three remaining valid species of *Scomberoides* leaves no doubt that he was able

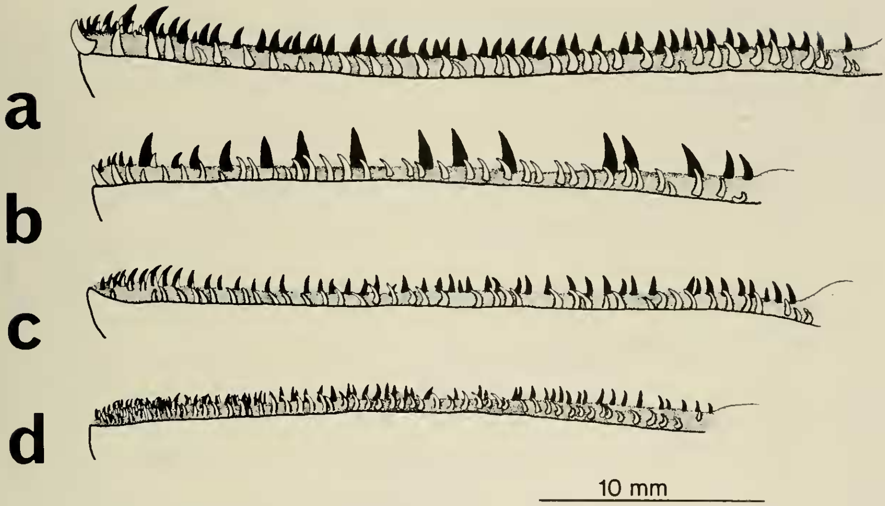

Figure 4. Dentary teeth of adult *Scomberoides* species: a, *S. commersonianus*; b, *S. tala*, c, *S. lysan*, d, *S. tol*. Data as in figure 2. Teeth of inner row shown in black.

to distinguish them. It is obvious from his description of *S. tala* that he would not have confused it with *S. tol*. At some time type labels or MNHN catalog numbers must have become inadvertently mixed. Since the description of *S. tol* was based in part on specimens from Malabar, the two specimens of that species labeled as types of *S. tala* are here designated putative paralectotypes of *Scomberoides tol* (Cuvier).

Russell's poor figure of "toloo parah," upon which the original description of *Chorinemus toloo* is based, cannot be positively identified as *S. tala*, although it most closely resembles that species. Weber and De Beaufort (1931) included *S. toloo* in their synonymy of *Scomberoides tala*; the figure of *Chorinemus toloo* published in Day's *Fishes of India* is clearly referable to *S. tala*.

Jordan and Seale distinguished their new genus and species, *Eleria philippina*, from *Scomberoides* solely on the basis of strong symphyseal canines on the lower jaw. They apparently were unaware that such canines are typically present in the young of *S. tala*.

The description and figure of *Chorinemus hainanensis* leave no doubt as to the identity of this nominal species. In their description, Chu and Cheng emphasized the absence of spots on side of body. Like a number of authors, they were not cognizant of the fact that these spots frequently fade completely.

Description. Characters given in the generic description are not repeated here. Frequency distributions of selected meristic characters are given in table 2. Dorsal-fin rays VI-VII + I, 19–21; anal-fin rays II + I, 17–19; pectoral-

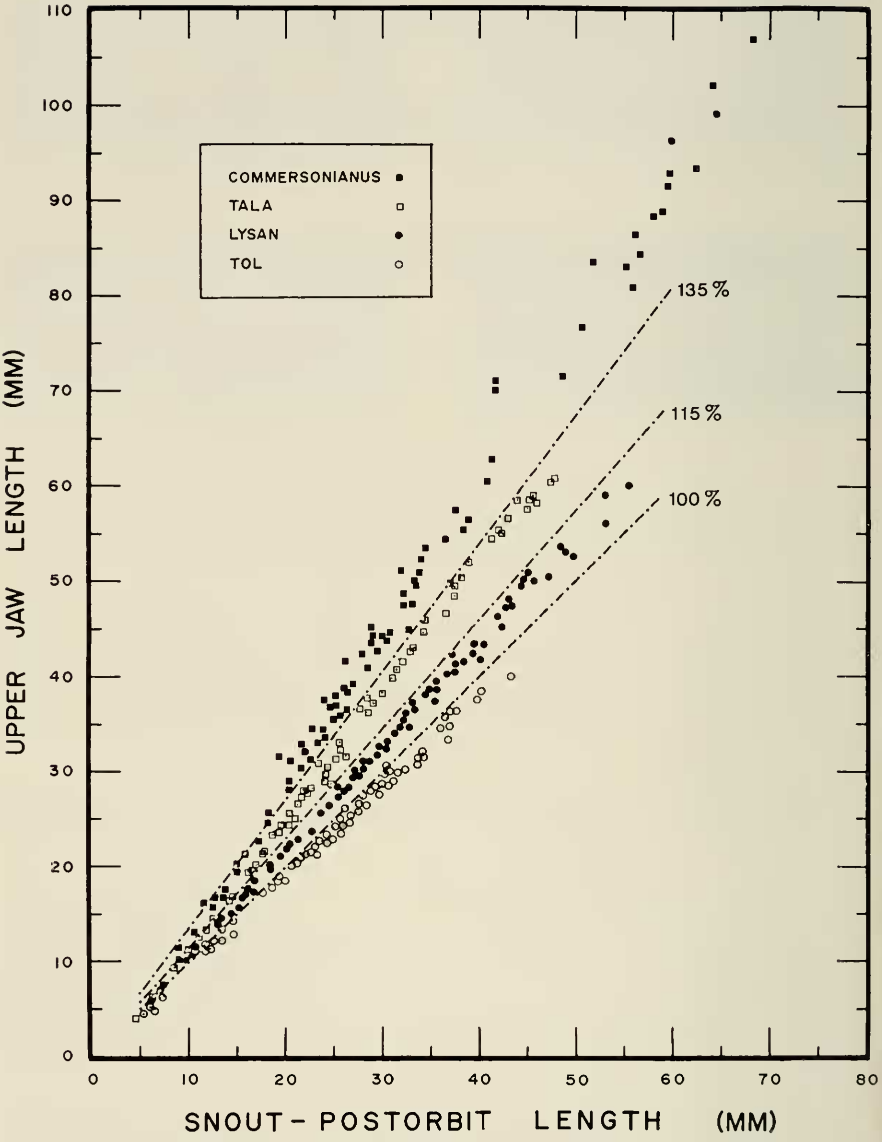

Figure 5. Relationship of upper jaw length to snout-postorbit length in *Scomberoides* species. Dashed lines represent upper jaw length as percent snout-postorbit length.

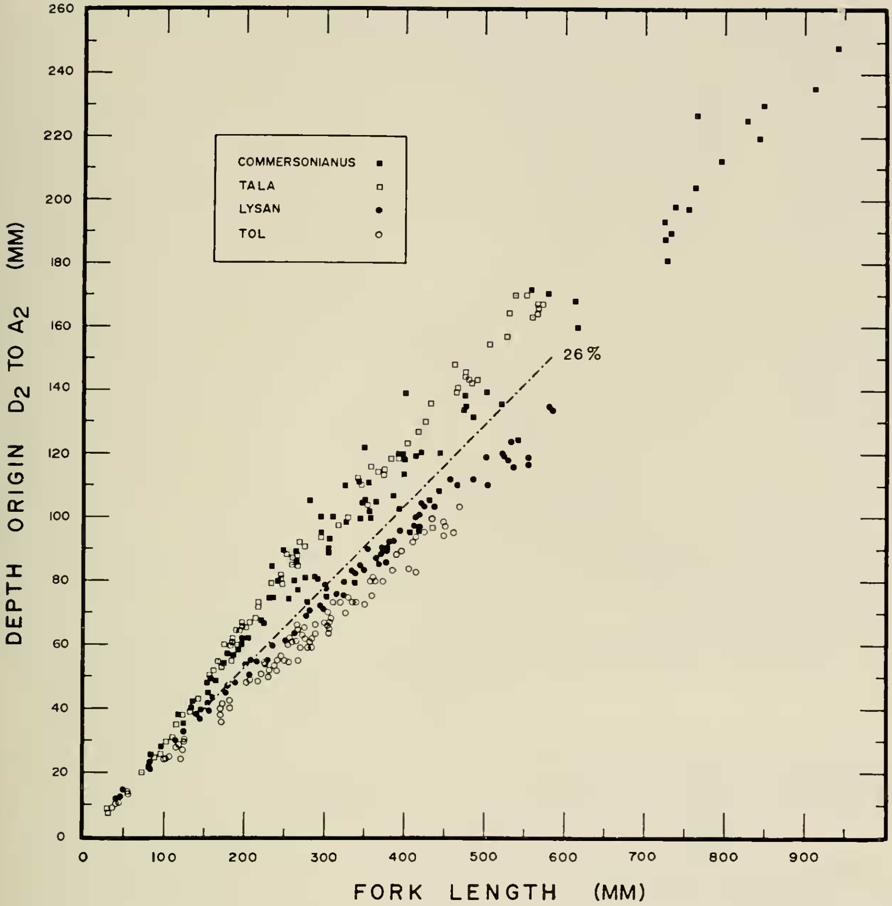

Figure 6. Relationship of body depth to fork length in *Scomberoides* species. Dashed line represents depth as percent fork length.

fin rays I, 16–17. Gillrakers 1–3 + 7–11 = 11–15. Upper jaw extending slightly beyond posterior margin of eye in adults (fig. 2b). Scales lanceolate (fig. 3c). Inner row of dentary teeth distinctly larger than outer row teeth in adults (fig. 4b); dentary typically with one or two pair of symphyseal canines in young; young with dentary teeth of outer row numerous and considerably more closely spaced than inner row teeth.

Proportional measurements apply only to specimens more than 150 mm. fork length (FL), and are in percent FL unless otherwise stated. Depth (origin D_2 to A_2) 29.0–34.9; height dorsal-fin lobe 14.6–18.0; height anal-fin lobe 13.1–16.2; upper jaw 54.3–61.6 percent head length; snout 26.1–30.1 percent head length.

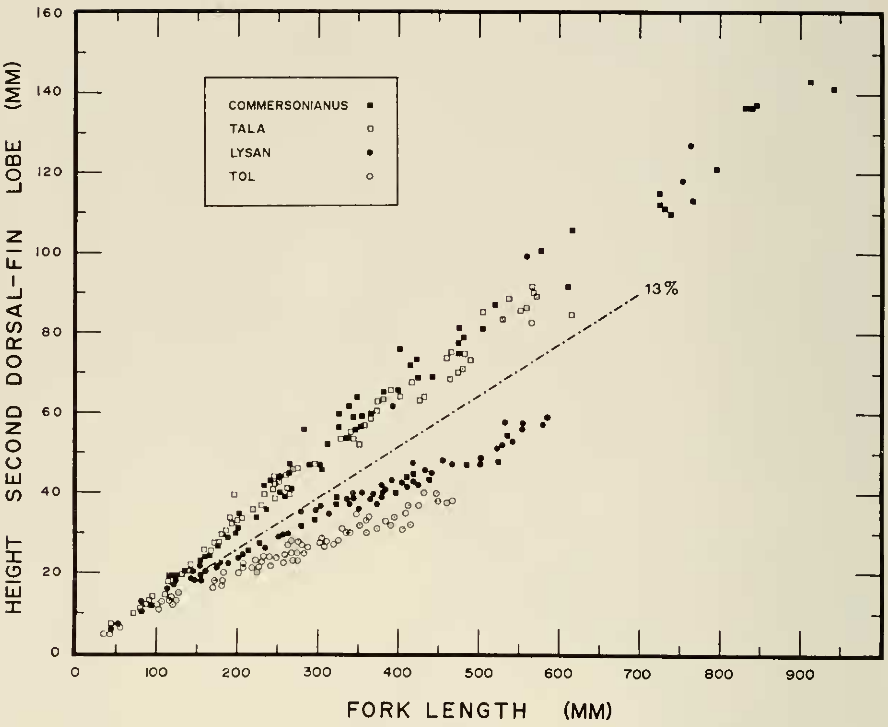

Figure 7. Relationship of dorsal-fin lobe height to fork length in *Scomberoides* species. Dashed line represents dorsal-fin lobe height as percent fork length.

Pigmentation. Sides with 4 to 8 vertically elongate blotches, most of them intersecting lateral line. Dorsal and anal fins uniformly pigmented. Life coloration not observed.

Distribution. Widely distributed throughout the Indo-Australian Archipelago, and the Bay of Bengal in the Indian Ocean. Although more collections are needed, the apparent absence of the species from the western Indian Ocean, Red Sea, and Persian Gulf appears to be real. *Scomberoides tala* is apparently restricted to neritic waters, and does not occur east of the New Guinea-Solomon Islands region.

Material (110 specimens, 31–615 mm. FL from 45 collections). CEYLON: TABL 107365 FJS 69–27 (2: 295–464), S-V 69–77 (1: 560), S-V 69–156 (1: 116, cleared and stained), TABL 107712 CCK 69–43 (12: 244–490), CCK 69–45 (3: 517–567), CCK 69–53 (4: 265–474), CCK 69–54 (2: 197–565), CCK 69–89 (8: 366–483), CCK 69–94 (1: 505), CCK 69–104 (2: 529–551), CCK 69–111 (1: 568). INDIA: Malabar, MNHN A. 6588 (315, lectotype of *Chorinemus tala*); Madras, AMS B. 8124 (1: 197); Calcutta, AMS B. 8093 (1: 115). BURMA: Maungmagan Island, SU 33635 (2: 91–95). ANDAMAN ISLAND: AMS I. 68 (1: 57). GULF OF THAILAND: GVF station 57–90 (1: 87), GVF station 57–99 (1: 167), GVF-1470 (4: 185–214), GVF-1503 (1: 176), TABL 107040 GVF-1512 (5: 190–219), GVF-2195 (1: 45), GVF-2197 (3: 31–71), GVF-2203 (1: 131), GVF-2222 (3: 183–198), GVF-2497 (2: 159–161), GVF-2540 (1: 345), GVF-2546 (12: 219–275). MALAYSIA: Penang, TABL 107266 FJS 69–79 m. (3: 168–183). PHILIPPINES: Luzon, USNM 65339 (1: 265), 149803 (3: 110–132), 149804 (1: 80); Batangas Prov., CAS uncataloged (6: 135–172); Manila Bay, CAS uncataloged (1: 165); Leyete, USNM 149805 (1: 178), 149811 (1: 178); Mindanao, USNM 55990 (1: 271); Matnog Bay, USNM 194913 (1: 218); Balabac Island, AMS I. 10478 (1: 220); Southern Negros, USNM 51945 (98, holotype of *Eleria philippina*), 75729 (1: 112), SU 9131 (2: 103–111). JAVA: USNM 72616 (2: 157–161), 72617 (1: 118), 72618 (1: 109), 72619 (1: 114). AUSTRALIA: Northern Territory, Port Darwin, AMS I. 5291–2 (2: 76–100), IA. 3639 (1: 67); Gulf of Carpentaria, Groote Eylandt, USNM 173957 (5: 317–339); Queensland, Cape York, BMNH 1879.5.14.282 (1: 381); Fitzory River Estuary, AMS IB. 1249 (1: 73). NEW BRITAIN: 4°19′S., 152°1′E., GVF station HK-130 (1: 615). SOLOMON ISLANDS: Bougainville, AMS IB. 1458 (1: 219).

Scomberoides lysan (Forskål).

(Figures 1c, 2c, 3b, 4c, 5–7, 19; tables 2–3.)

Scomber lysan Forskål, 1775, p. 54 (type locality Djeddae and Lohajae, Red Sea).

Scomber forsteri Bloch and Schneider, 1801, p. 26 (type locality Pacific Ocean [based on *Scomber maculatus* Forster MS]).

Lichia tolooparah Rüppell, 1828, p. 91 (type locality Massawa, Red Sea).

Chorinemus sanctipetri Cuvier *in* Cuvier and Valenciennes, 1831, p. 379 (279) (type locality Malabar coast).

Chorinemus moadetta Ehrenberg *in* Cuvier and Valenciennes, 1831, p. 382 (282) (based on an unpublished drawing by Ehrenberg of a fish from the Red Sea).

Chorinemus mauritianus Cuvier *in* Cuvier and Valenciennes, 1831, p. 382 (282) (type locality l'Isle-de-France [=Mauritius Island]).

Scomber maculatus Forster, 1844, p. 195 (type locality Tahiti).

Chorinemus orientalis Temminck and Schlegel, 1844, p. 106, pl. 57, fig. 1 (type locality Nagasaki, Japan).

Thynnus moluccensis Gronovius *in* Gray, 1854, p. 121 (type locality Insulas Moluccenses).

Scomberoides formosanus Oshima (*non* Wakiya), 1925, p. 349, pl. 1, fig. 1 (type locality Tôkô, Formosa).

Scomberoides oshimae Whitley, 1951, p. 65 (replacement name for *Scomberoides formosanus* Oshima, 1925, preoccupied).

Nomenclature. The description of *S. lysan* is inadequate for positive identification, but the following statements given by Forskål suggest that he did not have *S. commersonianus* (= '*lysan*' of recent workers): (1) scales lanceolate (in "*S. lysan*" they are usually referred to as ovate or broadly lanceolate); (2) "about the lateral line there are obsolete [?indistinct] dark spots"; (3) dentes [teeth] numerous, small. Rüppell (1828), who set out especially to clarify the identities of Forskål's Red Sea fishes, applied the name 'lysan' to *S. commersonianus*. His application of the name, however, was based on the fact that native fishermen referred to that species as "lysan." Smith (1968, p. 174) has clearly shown that native names of Red Sea fishes were often not specific. Cuvier and Valenciennes (1831) did not believe the description of *S. lysan* was sufficiently diagnostic for positive identification. They did, however, state that since Forskål's description contained no mention of a dark blotch in the second dorsal fin, they were hesitant to refer it to their *Chorinemus moadetta*. Günther (1860) and all subsequent workers have regarded *S. lysan* as a senior synonym of *S. commersonianus*.

Klausewitz and Nielsen (1965, pl. 25) have published an excellent photograph and radiograph of the 216 mm. SL lectotype (ZMC 44) of *Scomber lysan*, reproduced without comment in Smith (1970). The most distinctive feature of the lectotype is the position of the maxilla, which ends below the middle of the eye. It is also apparent from the radiograph that the snout has been pushed in on the dried skin, giving the snout an atypically blunt appearance. Since the maxilla extended well beyond the posterior margin of the orbit in all our specimens, we suspected that the *'lysan'* of recent authors was not the same species as the lectotype. Accordingly we wrote Dr. Jørgen Nielsen and asked him to examine the lectotype for us. The following information, largely provided by Dr. Nielsen, is sufficient to identify the lectotype as conspecific with *S. tolooparah* of recent workers: (1) Although there are no teeth left in the outer dentary row, judging from the sockets the missing teeth were the same size and number as those of the inner row, which excludes *S. tala* (see fig. 4); (2) comparison of the premaxillary teeth also excludes *S. tala*; (3) there are no symphyseal canines left. Symphyseal canines are never present in *S. lysan*, and usually are still retained in specimens of *S. commersonianus* and *S. tala* at this size; (4) the length of the upper jaw is 21 mm.; the dentary is 30 mm. The 1:1.5 ratio between the length of the upper jaw and dentary agrees fairly well with similar sized specimens of *S. tolooparah* and is sufficiently different to exclude *S. commersonianus*; (5) the scales of the paralectotype and the lectotype are the same size and form. Comparison of a small patch of skin (scales included) removed from the paralectotype just anterior to the spinous dorsal fin with scales from the same area of the four species of *Scomberoides* is sufficient to exclude *S. tol*, *S. commersonianus*, and, with less confidence, *S. tala*. The most diagnostic feature of these scales is their strongly lanceolate posterior margins (see fig. 3).

Unfortunately, the name *S. lysan* (applied to *S. commersonianus* by recent authors) must be retained as a senior synonym of the widely used *S. tolooparah.* It would be difficult to justify suppression of the name, however, since it is not simply an overlooked synonym of *S. tolooparah. Scomberoides forsteri* is also a senior synonym of *S. tolooparah*; and *S. sanctipetri,* a junior synonym, has frequently been recognized as a valid species. Although carangids are commercially important fishes, most genera have not been adequately revised, and consequently many of the names currently in use may eventually prove to be synonyms.

Although the descriptions of *Scomber forsteri* and *S. maculatus* are poor, they apply best to *S. lysan.* Since the type locality of *S. maculatus* (and thus that of *S. forsteri* as well) is Tahiti, an area from which only *S. lysan* is known, there can be little doubt as to the specific identity of either nominal species. The characters given for *Chorinemus moadetta,* and comparison of it in the original description with Forskål's *S. lysan,* leaves no doubt that it too is a junior synonym of *S. lysan.*

Smith (1970) presents photographs of the holotypes of *Lichia tolooparah* (NFIS 386) and *Chorinemus sanctipetri* (MNHN A. 6587). They are both clearly synonyms of *S. lysan.* Likewise, the original descriptions and figures of *Chorinemus orientalis* and *Scomberoides formosanus* agree well with *S. lysan.* The description and insular type locality of *Chorinemus mauritianus* are also sufficient to identify it as conspecific with *S. lysan.*

We have not examined the type of *Thynnus moluccensis,* but according to Wheeler (1958, p. 220) it is a synonym of *Chorinemus sanctipetri* (= *S. lysan*). The 142 mm. SL holotype bears the catalog number BMNH 1853. 11.12.29.

DESCRIPTION. Characters given in the generic description are not repeated here. Frequency distribution of selected meristic characters are given in table 2. Dorsal-fin rays VI-VII+I, 19–21, anal-fin rays II-I, 17–19; pectoral-fin rays I, 16–17. Gillrakers 3–8 + 15–20 = 21–27. Upper jaw extending to or slightly beyond (in large adults) posterior margin of eye (fig. 2c). Scales lanceolate (fig. 3b). Inner and outer row of dentary teeth subequal in adults (fig. 4c); dentary without symphyseal canines; young with dentary teeth of outer row numerous and considerably more closely spaced than inner row teeth.

Proportional measurements apply only to specimens more than 150 mm. fork length (FL), and are in percent FL unless otherwise stated. Depth (origin D_2 to A_2) 20.9–27.3; height dorsal-fin lobe 9.1–14.2; height anal-fin lobe 7.7–11.6; upper jaw 50.3–54.6 percent head length; snout 27.8–31.8 percent head length.

PIGMENTATION. Sides of adults with a double series of 6 to 8 dusky roundish blotches above and below lateral line, occasionally connected by narrow isthmus. Distal half of dorsal-fin lobe abruptly and heavily pigmented; anal-fin lobe white or pale yellow, often with interradial membranes of several anterior rays black, especially in large individuals. In life, body gray-green above, silvery gray to midline, silvery white below.

Distribution. Widely distributed throughout the Red Sea, Indian Ocean, Indo-Australian Archipelago and central Pacific Ocean including Hawaii and the Marquesas Islands. *Scomberoides lysan* is the only species of *Scomberoides* that occurs east of the Solomon Islands and frequents entirely oceanic islands in the Indian Ocean, *e.g.*, Seychelles and Chagos Archipelago. The other species of *Scomberoides* are generally restricted to neritic habitats. This suggests a fundamental difference in the biology of *S. lysan.*

Material (276 specimens, 20–585 mm. FL from 109 collections). TANZANIA: Zanzibar, TABL 105602 (1: 281). MADAGASCAR: USNM 171034 (1: 336), TABL uncataloged station JR-68 (1: 54). MAURITIUS ISLAND: USNM 118407 (13: 256–403). COMORO ISLANDS: TABL uncataloged station FT-9 (2: 45–46), TABL uncataloged station HA-8 (1: 123), HA-10 (1: 52). ALDABRA ISLAND: TABL uncataloged station HA 67–56 (1: 385). CHAGOS ARCHIPELAGO: Diego Garcia Atoll, TABL uncataloged station HA 67–42 (2: 83–113), HA 67–43 (3: 146–154). INDIA: Malabar, MNHN A. 5893 (480, holotype of *Chorinemus sanctipetri*); Madras, AMS B. 8091 (3: 110–128). CEYLON: TABL 107364 FJS 69–27 (2: 412–523), S-V 69–123 (8: 177–303), S-V 69–128 (2: 123–161, cleared and stained), S-V 69–152 (9: 278–355), PCH 69–201 (1: 541), PCH 69–224 (1: 279), PCH 69–225 (1: 381), PCH 69–228 (1: 585), CCK 69–9 (1: 525), CCK 69–49 (4: 467–530), CCK 69–53 (1: 339), CCK 69–110 (1: 343), CCK 69–113 (2: 370–535), CCK 69–130 (1: 555). SOUTH CHINA SEA: Hainan Island, USNM 94780 (1: 178). TAIWAN: USNM 192563 (1: 194). OKINAWA ISLAND: USNM 72093 (2: 125–211). PHILIPPINES: Luzon, USNM 139573 (2: 33–38), 149797 (1: 47), 149800 (1: 31), 168276 (1: 215), 168277 (1: 220), 191855 (2: 29–48), 191888 (11: 45–73), 191889 (11: 83–103), 191891 (6: 76–116), 191894 (4: 44–100), 191896 (2: 200–213), 191907 (1: 76), 191913 (1: 54); Burias Island, USNM 194916 (1: 232); Busanga Island, USNM 191884 (3: 42–56); Linacapan Island, USNM 191893 (2: 66–92); Pandanon Island, USNM 191910 (2: 89–97); Mindoro, USNM 149799 (3: 66–79), 191902 (1: 73), 191908 (1: 96); Samar, USNM 191859 (4: 190–196); Leyete, USNM 191886 (11: 64–188); Palawan, USNM 191887 (19: 26–187), 191897 (4: 81–185), 191905 (1: 39); Cuyo Island, USNM 191911 (2: 67–81). BORNEO: Sandakan Bay, USNM 191901 (3: 83–109). AUSTRALIA: Northern Territory, Bedwell Point, AMS IA. 7679–80 (2: 136–200); Gulf of Carpentaria, Sir Edward Pellew Group, AMS IA. 1488 (1: 129), IA. 2559 (1: 144); Queensland, AMS A. 12495 (1: 141); Cape York, AMS I. 9712–4 (3: 206–217); Barrier Reef, USNM 176914 (6: 129–194); Townsville, AMS IA. 2324–5 (2: 150–164); Lindeman Island, AMS IA. 6288 (1: 290), IA. 6289–90 (2: 112–158), IA. 6647 (2: 110–128), IA.

7498–7501 (4: 51–75), IA. 7887 (1: 88); Hayman Island, AMS IA. 6126–7 (4: 35–132); Burdekin River, I. 5314–5 (2: 175–187), A. 18302 (1: 157); New South Wales, Sydney, MKT AMS IB. 4232 (1: 290), USNM uncataloged station BBC 1464 (1: 295); Gafton, AMS I. 15594–001 (1: 65). NEW GUINEA: Aroma, AMS IA. 5738 (3: 33–69); Hula Village, AMS IB. 1706 (1: 160); Bat Island, Purdy Archipelago, AMS IB. 1523 (1: 82). NEW BRITAIN: GVF station HK-29 (1: 297), GVF station HK-130 (1: 418). SOLOMON ISLANDS: Bougainville, TABL uncataloged *Te Vega* Expedition, Cruise 6, station 247 (1: 155); Ontonga Java Island, AMS IA. 3696 (1: 355). PALAU ISLAND: GVF-546 (1: 81), GVF-591 (1: 83), GVF-1971 (2: 189–205), GVF station 59–708 (11: 373–442), GVF station 59–710 (2: 369–410), GVF station 59–724 (2: 365–379). MARIANA ISLAND: Saipan, USNM 154647 (1: 54). MARSHALL ISLANDS: USNM 66022 (1: 40), 66024 (1: 37), 66025 (1: 30), 142040 (1: 580), 142041 (2: 30), 142042 (2: 28–32), 163134 (1: 26), 165648 (2: 78–80), 179433 (1: 63). GILBERT ISLANDS: USNM 66021 (1: 60); Onotoa, USNM 167428 (2: 380–415); Arorae, AMS IB. 6618 (1: 25); Nauru, AMS IA. 6999 (1: 375). ELLICE ISLAND: AMS IA. 5531 (1: 215); Funafuti, USNM 66020 (1: 96), AMS I. 3562 (1: 495). PHOENIX ISLANDS: Canton Island, USNM 115330 (1: 456). SAMOA ISLANDS: Apia, USNM 52361 (3: 219–240). NEW HEBRIDES ISLANDS: Malehuka, AMS I. 11294 (1: 162). FIJI ISLANDS: Suva, USNM 66023 (2: 176–177). TONGA ISLANDS: Vavau, USNM 66019 (1: 103); Tonga, TABL uncataloged, *Te Vega* Expedition, Cruise 8, station 308 (2: 215–227). SOCIETY ISLANDS: Tahiti, GVF-1155 (1: 324), GVF station 57–6 (1: 296). TUAMOTU ARCHIPELAGO: Rangiroa, USNM 66018 (2: 84–135); Takaroa, GVF station 56–?? (1: 299); Raroia, GVF-87 (3: 502–555). MARQUESAS ISLANDS: Nukahiva, USNM 66016 (1: 416), 66017 (3: 184–215); Hiva Oa, USNM 186329 (2: 33–38). LINE ISLANDS: Palmyra Island, GVF station 51–41 (5: 350–419), GVF station 51–44 (4: 140–157); Christmas Island, USNM 19238 (3: 402–415). JOHNSTON ISLAND: USNM 26825 (1: 440). HAWAIIAN ISLANDS: Hawaii, USNM 78073 (5: 26–69), 82818 (1: 279), 83429 (1: 227); Oahu, SU 3270 (5: 172–220), 7647 (3: 103–190), 53345 (1: 20), USNM 55082 (1: 357), 55371 (1: 141), 88161 (1: 166), 88162 (3: 172–255), 126691 (1: 174), 151615 (3: 191–260).

Scomberoides tol (Cuvier).

(Figures 1d, 2d, 3d, 4d, 5–7, 14d, 19, 20b, 21c, 22c; tables 2–3.)

Chorinemus tol CUVIER *in* Cuvier and Valenciennes, 1831, p. 385 (type localities Pondichery; Malabar coast; Amboine; Ile de Bourou).

Scomberoides formosanus WAKIYA, 1924, p. 236, pl. 38, fig. 3 (type locality Kii, Formosa).

NOMENCLATURE. The original description of *Chorinemus tol* is sufficiently diagnostic for positive identification (see also discussion under *S. tala*). Likewise the statement "scales linear, pointed at both ends" given in the description of *S. formosanus* could apply only to *S. tol* Cuvier. F. H. Berry has examined the 130 mm. SL holotype (FMNH 59499), and made his data available to us.

DESCRIPTION. Characters given in the generic description are not repeated here. Frequency distributions of selected meristic characters are given in table 2. Dorsal-fin rays VI-VII + I, 19–21; anal-fin rays II + I, 18–20; pectoral-fin rays I, 15–18. Gillrakers 4–7 + 17–20 = 21–26. Upper jaw does not extend to posterior margin of eye (fig. 2d). Scales slender, needlelike (fig. 3d). Inner and outer row of dentary teeth subequal in adults (fig. 4d); dentary typically with one or two pairs of symphyseal canines in young; young with dentary teeth of outer row only slightly more numerous and closely spaced than inner row teeth.

Proportional measurements apply only to specimens more than 150 mm. fork length (FL), and are in percent FL unless otherwise stated. Depth (origin D_2 to A_2) 20.0–24.7; height dorsal-fin lobe 7.7–11.2; height anal-fin lobe 6.3–8.8; upper jaw 42.6–49.3 percent head length; snout 29.1–32.8 percent head length.

PIGMENTATION. Sides of adults with 5 to 8 oval or vertically oblong blotches, the first 4 or 5 of which intersect lateral line. Distal half of dorsal-fin lobe abruptly and heavily pigmented; anal-fin lobe usually immaculate, white in life. In life, body white ventrally, bluish dorsally; lateral blotches black, faint or absent in young.

DISTRIBUTION. Widely distributed throughout the Indo-Australian Archipelago and Indian Ocean. Although we have not examined specimens, the species has been reliably reported from the Red Sea. *Scomberoides tol* is apparently restricted to neritic waters, and does not occur east of the New Guinea-Solomon Islands region.

TYPE MATERIAL. MNHN A. 6605 (150, here designated lectotype of *Chorinemus tol*) Malabar. Paralectotypes as follows: MNHN B. 2650 (2: 135–147, removed from A. 6605), B. 5542 (dried skin, not measured) Pondichery, A. 6585 (1: 170) Bourou Island, A. 6620 (1: 119) Amboine. MNHN A. 6587 (2: 296–302, putative paralectotypes) Malabar (see discussion under *S. tala*). FMNH 59499 (130 mm. SL, holotype of *S. formosanus*) Kii, Formosa.

OTHER MATERIAL (142 specimens, 20–468 mm. FL from 66 collections). SOUTH AFRICA: Durban, TABL uncataloged FJS 69–1 (7: 224–267). MOZAMBIQUE: Ponta Mabonl, TABL uncataloged FJS 69–5 (1: 173); Polana, TABL uncataloged FJS 69–12 (1: 208); Mecaneta, TABL uncataloged FJS 69–14 (3: 225–232). KENYA: Mombasa, TABL uncataloged *Anton Bruun* cruise 9, station FT-2 (2: 271–276). MADAGASCAR: USNM 171055 (1: 185), TABL uncataloged JR-27 (3: 171–173), JR-70 (1: 120), TABL uncataloged *Anton Bruun* cruise 7, Tulear Harbor, (1: 124). PERSIAN GULF: USNM 147819 (1: 20), 148074 (1: 323). INDIA: Bombay, TABL uncataloged FHB

66–1 (4: 37–55); Kerala State, Cochin, TABL uncataloged FHB 66–53 (1: 127); Madras State, AMS B. 8045 (1: 171); Cape Comorin, TABL uncataloged FHB 66–46 (1: 222), FHB 66–49 (2: 264–330); Porto Nova, TABL uncataloged FHB 66–17 (2: 282–284). CEYLON: FJS 69–14 (3: 225–232), TABL 107707 S-V 69–86 (4: 262–284), S-V 69–123 (8: 240–390), TABL 107363 S-V 69–126 (8: 268–450), S-V 69–128 (6: 107–131.5, 2 cleared and stained), PCH 69–180 (1: 326), PCH 69–185 (10: 102–107), PCH 69–202 (2: 108–126), PCH 69–237 (1: 310), PCH 69–266 (4: 358–373), PCH 69–292 (3: 146–154), CCK 69–9 (1: 340), CCK 69–43 (1: 181), CCK 69–73 (1: 395), CCK 69–91 (1: 242), CCK 69–94 (1: 468), CCK 69–113 (3: 410–426), CCK 69–129 (8: 351–460). MALAYSIA: Penang, TABL uncataloged FJS 69–74 m. (2: 209–219). GULF OF THAILAND: GVF station 13B-C (6: 209–246) GVF-1541 (7: 141–203), GVF-2546 (8: 269–320), GVF-2655 (2: 117–119). TAIWAN: USNM 76607 (8: 41–149), SU 7317 (1: 169), 20997 (2: 203–218). JAPAN: Kagoshima, SU 23774 (3: 86–117). PHILIPPINES: Luzon, USNM 56329 (5: 105–224), 168275 (1: 207), 168281 (1: 372), 168282 (1: 331), USNM uncataloged (out of USNM 191896) (1: 115), 191899 (1: 156), 191906 (1: 77), 191909 (1: 89), 191912 (1: 89), AMS I. 10539 (1: 215); Leyte, USNM 149796 (1: 38); Cebu, USNM 191900 (2: 123–134); Panay, USNM 149794 (1: 30), 191898 (1: 105); Mindanao, USNM 55995 (1: 244), 58011 (2: 143–144), 59004 (1: 149), 168283 (1: 348). JAVA: Batavia, USNM 726211 (2: 122–140), 72612 (1: 171), 72613 (1: 145), 72614 (1: 130), 72615 (2: 162–208). AUSTRALIA: Western Australia, Onslow, WAM P. 15488–90 (3: 110–174); Port Hedland, AMS IB. 1638 (1: 128); Gulf of Carpentaria, 16°53′S., 139°21′E., AMS I. 15557–118 (5: 87–172); Queensland, Barrier Reef, USNM uncataloged (out of USNM 176914) (1: 171); Palmers Island, AMS I. 2962–3 (2: 90–91); Hayman Island, AMS IA. 6373 (1: 221). NEW GUINEA: Sumarai District, AMS IA. 5740 (1: 235). SOLOMON ISLANDS: Bougainville, TABL uncataloged *Te Vega* Expedition, cruise 6, station 246 (2: 43–44); Malaita Island, AMS I. 15360–056 (1: 350).

Scomberoides spinosus (Smirnov).

(Figure 8.)

Palaeoscomber spinosus Smirnov, 1936, p. 49–59, pl. 7, figs. 31–32 (type locality Zuramakent Horizon of the Upper Maikop deposits, Northeastern Caucasus).

Danil'chenko (1960) has given a detailed redescription of *Palaeoscomber spinosus* and convincingly demonstrated that it is a species of carangid, although originally believed to represent a new genus and subfamily of Scombridae (Smirnov, 1936). In reassigning *P. spinosus* to *Oligoplites*, Danil'chenko emphasized the peculiar needlelike scales which he regarded as a "characteristic sign" of the genus. He did not compare it with *Scomberoides tol*, apparently

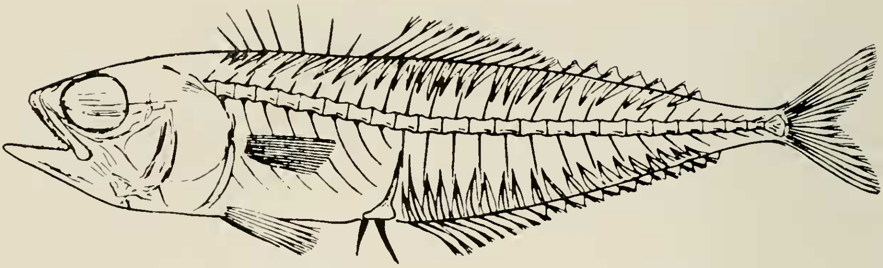

Figure 8. Diagrammatic sketch of *Palaeoscomber spinosus* Smirnov (after Danil'chenko, 1960).

unaware that its scales are identical to those of *Oligoplites.* Although we have not examined specimens of *P. spinosus,* and therefore do not include a description, we believe it is a species of *Scomberoides* closely related to *S. tol.* The number of dorsal-fin rays (VI-VII + I, 20) and predorsal bones (3) reported for *P. spinosus* apply best to a species of *Scomberoides.* Likewise, the relatively short upper jaw (47 to 48 percent HL) and general configuration of the maxilla suggest *S. tol* rather than a species of *Oligoplites* (compare figs. 2d and 8).

The four fossils upon which the description is based are from the Zuramakent Horizon of the Upper Maikop deposits (Lower Miocene) in the Northeastern Caucasus. According to Danil'chenko (1960), only 3 of 18 genera examined from this deposit do not represent recent genera. The recent species *Scomber japonicus* Houttuyn is also present. The characters of *Oligoplites* and its present distribution (western Atlantic and eastern Pacific) suggest that it evolved from a *Scomberoides*-like ancestor that reached the New World via the Pacific (see discussion under Relationships and Zoogeography Section). It seems more logical in view of the geographical location and recent nature of the Upper Maikop fauna that *P. spinosus* represents a genus present in the Indian Ocean rather than one that is restricted to the western Atlantic and eastern Pacific oceans.

Two characters mentioned in the redescription of *P. spinosus* require comment. (1) The supramaxilla is said to be absent. The small supramaxilla of *Scomberoides* could easily be lost or overlooked in a fossil. (2) The vertebral count is given as 10 + 15. In his discussion of methods Danil'chenko (1960) stated that the vertebrae were counted as in recent fishes (the urostyle is treated as a separate vertebra), yet his diagrammatic drawing of *P. spinosus* (here reproduced as fig. 8) clearly shows 10 + 16 vertebrae. We believe the count of 10 + 15 is an error. Berry (1968, p. 148) stated that the number of vertebrae is intraspecifically very constant in all Carangidae. One exception that he noted was one specimen of *Oligoplites saurus inornatus* Gill with 10 + 17 vertebrae;

19 others had 10 + 16. We have made numerous vertebral counts of all species of *Oligoplites* and *Scomberoides* and except for the specimen mentioned above, all have 10 + 16 vertebrae.

The available material of *Scomberoides spinosus* should be carefully compared with similar sized specimens of *S. tol.* We tentatively regard them as specifically distinct because several of the proportional measurements given for *S. spinosus* do not agree with our specimens of *S. tol.*

Oligoplites Gill, 1863

Oligoplites Gill, 1863, p. 166 (type species: *Scomber saurus* Bloch and Schneider, 1801, by subsequent designation of Jordan, 1917, p. 324).

Leptoligoplites Fowler, 1944, p. 226 (as a subgenus of *Oligoplites*; type-species: *Oligoplites refulgens* Gilbert and Starks, 1904, by original designation).

The carangid genus *Oligoplites* comprises five species of tropical and subtropical marine fishes restricted to the eastern Pacific and western Atlantic oceans. Only one species, *O. saurus*, occurs in both oceans. Parenthetically, it should be noted that in his excellent review of the zoogeographic relationships of tropical American marine shore fishes, Rosenblatt (1967, p. 590) has perpetuated a misconception by reporting *Oligoplites* from the eastern Atlantic. The genus is largely confined to inshore, neritic waters, and the young are sporadic invaders of coastal freshwater habitats (Gunter and Hall, 1963; Miller, 1966; Gilbert and Kelso, 1971). Breder (1942) has made the interesting observation that the young of *Oligoplites saurus* 27 to 34 mm. SL, which appear on the west coast of Florida during June and July, frequently drift passively at the surface head-down or twisted in a most unfishlike manner. He noted that their behavior and general appearance almost perfectly mimicked a floating dead leaf. The young of *Scomberoides lysan* have been observed exhibiting similar behavior (Major, 1973). The largest species of *Oligoplites* seldom, if ever, exceed 40 cm. fork length. In Central and South America they are commonly sold in fish markets. F. H. Berry *in* McClane (1965, p. 477) has reported *Oligoplites altus* (as *O. mundus*) to be an exceptionally strong and stubborn fighter on light tackle.

Oligoplites shows a striking external resemblance to the allopatric Indo-Pacific genus *Scomberoides*, and together they constitute the subfamily Scomberoidinae (=Chorineminae) of recent authors. Starks (1911) gives a detailed osteological comparison of these two genera. The adults of *Scomberoides* have a series of prominent spots or bars on the sides that is absent in *Oligoplites*, although faint bars may occasionally be present in *O. saurus*. The genus was last reviewed by Schultz (1945). Several junior synonyms overlooked in that work are included in our synonymies. The species that we recognize may be

Table 4. *Frequency distribution of meristic characters in* Oligoplites *species.*

Species	Upper Gill Rakers 2	3	4	5	6	7	8	N	x̄	Lower Gill Rakers 8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	N	x̄
altus	2	23	31	9	—	—	—	65	3.7	1	9	14	17	10	14	—	—	—	—	—	—	—	—	—	65	11.0
palometa	—	1	14	22	—	—	—	37	4.7	—	—	—	8	16	12	1	—	—	—	—	—	—	—	—	37	12.2
saliens	—	—	2	12	26	1	—	41	5.6	—	—	—	—	—	—	—	—	—	3	9	23	6	—	—	41	18.8
refulgens	—	—	—	—	9	33	4	46	6.9	—	—	—	—	—	—	—	—	—	—	—	10	15	15	6	46	20.4
saurus saurus	—	4	8	10	13	—	—	35	4.9	—	—	—	—	—	7	24	4	—	—	—	—	—	—	—	35	13.9
saurus inornatus	—	—	—	13	8	4	—	25	5.6	—	—	—	—	—	—	6	9	9	—	1	—	—	—	—	25	15.2

Species	Total Gill Rakers 11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	N	x̄	First Dorsal Spines IV	V	VI	N
altus	2	9	9	8	13	9	10	5	—	—	—	—	—	—	—	—	—	—	—	65	14.7	21	40	—	61
palometa	—	—	—	1	3	9	16	7	1	—	—	—	—	—	—	—	—	—	—	37	16.7	36	2	—	38
saliens	—	—	—	—	—	—	—	—	—	—	1	—	6	14	14	6	—	—	—	41	24.4	42	—	—	42
refulgens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	13	14	11	2	46	26.8	7	45	—	52
saurus saurus	—	—	—	—	—	—	7	6	8	13	1	—	—	—	—	—	—	—	—	35	18.8	1	34	2	37
saurus inornatus	—	—	—	—	—	—	—	—	—	4	8	7	5	—	1	—	—	—	—	25	21.7	—	24	1	26

Correlation of predorsal bones and pterygiophores of first dorsal spines
(predorsal bones + pterygiophores[1])

Species	4 + 5	4 + 6	5 + 4	5 + 5	6 + 4	N
altus	—	—	—	13	10	23
palometa	—	—	—	3	8	11
saliens	—	—	23	—	—	23
refulgens	1	—	—	33	1	35
saurus saurus	—	1	—	19	—	20
saurus inornatus	1	1	—	12	—	14

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[1] All dorsal pterygiophores bear a single spine.

Table 5. *Comparison of upper jaw length (expressed as percent HL) and body depth (expressed as percent FL) in* Oligoplites *species.*

Species	<150 mm. Range FL	N	Upper Jaw Length Range	Upper Jaw Length x̄	N	Depth Range	Depth x̄
altus	35–149	13	59–66	63.4	10	27–32	29.8
palometa	92–147	12	58–63	59.7	12	24–31	27.3
saliens	88–146	7	57–67	62.3	8	26–29	27.0
refulgens	44–148	35	41–46	43.6	36	18–22	19.9
saurus saurus	31–144	11	52–57	54.7	10	23–26	23.9
saurus inornatus	53–132	20	52–57	55.3	20	23–25	24.0

Species	>150 mm. Range FL	N	Upper Jaw Length Range	Upper Jaw Length x̄	N	Depth Range	Depth x̄
altus	154–379	65	58–70	64.3	47	27–38	32.0
palometa	160–392	26	59–64	61.6	26	26–34	29.2
saliens	165–390	34	62–68	65.3	33	27–31	28.8
refulgens	150–230	22	42–46	43.5	22	19–22	20.0
saurus saurus	165–285	26	52–57	54.3	26	24–27	25.2
saurus inornatus	200–257	7	52–57	54.6	7	25–28	26.8

identified by reference to the key and tables 4–5. We have not included segmented dorsal- and anal-fin ray counts because, as in *Scomberoides,* they are not useful in defining species.

Nomenclature. Schultz (1945) considered *O. inornatus* Gill the "genotype" of *Oligoplites,* however, no type-species designation was given in the original description. We believe that the action of Jordan (1917, p. 324) qualifies *Scomber saurus* Bloch and Schneider, 1801, as the type-species in accordance with provision (iv) of Article 68a of the International Code of Zoological Nomenclature (1964).

We concur with Schultz (1945, p. 330) that recognition of the subgenus *Leptoligoplites* on the basis of a few more gill rakers and elongate body is unjustified. Differences in dentition would be a much better basis upon which to establish subgenera if such were needed.

Description. Body moderately to strongly compressed. Adipose eyelids moderately to poorly developed. Body, except head, covered with needlelike embedded scales. Lateral-line scales not developed into scutes. Lateral line without side branches, straight except for slight curve over pectoral fin. Anterior rim of shoulder girdle smooth, without fleshy papillae or deep groove near isthmus. Premaxillae not protractile, connected anteriorly to snout at midline by a wide fleshy bridge. Swimbladder strongly bifid posteriorly, length of bifurcated portion of swimbladder equal to or greater than undivided part. Posterior dorsal- and anal-fin rays consisting of semidetached finlets, distal fourth to half of ray not connected by interradial membrane (unattached portion of rays increasing with growth); ultimate and penultimate rays more closely spaced than adjoining rays, fully connected by interradial membrane; none of dorsal- or anal-fin rays produced into long filaments. Pelvic fins relatively short, depressible into shallow abdominal grooves. Pectoral fins short, not falcate, 57 to 80 percent head length in adults. Upper jaw extends posteriorly from middle of eye to well behind orbital rim, 42 to 70 percent head length in adults.

Predorsal bones 4 to 6, rarely 4; dorsal-fin rays IV-VI (rarely VI) + I, 18 to 21; total dorsal-fin rays 23 to 27. Anal-fin rays II + I, 19 to 21. Pectoral-fin rays I, 15 to 17. Pelvic-fin rays I, 5. Vertebrae 10 + 16 to 17 (rarely 17) = 26; epipleural ribs 8–10. Branchiostegal rays 3 + 4 or 2½ + 4½ (epihyal + ceratohyal). Upper gillrakers 2 to 8; lower gillrakers 8 to 22; total gillrakers 11 to 29.

Fronto-supraoccipital crest low; temporal crest poorly developed, not extending forward to posterior rim of orbit and not reaching edge of cranium; preorbital region short. Epiotics broadly united along midline of cranium internally. Zygapophyses of exoccipital widely separated beneath foramen magnum. Parasphenoid not expanded into a broad, flattened plate posteriorly. Myodome with broad, posterior opening. Basioccipital without a pair of lateral processes on ventral surface. Ascending process of premaxilla short and triangular; maxilla long and slender, rather closely attached to premaxilla. Premaxillary spur absent. Supramaxilla absent. Interosseous space between dorsal arm of dentary and upper margin of articular minute or absent. Well developed teeth on dentary, premaxilla, palatines, and vomer; two distinct rows of dentary teeth (see discussion under Relationships and Zoogeography Section); symphyseal premaxillary and dentary teeth of juveniles not robust or caniniform. Mesopterygoids edentate. Pharyngeals not noticeably enlarged, covered with sharp, pointed teeth.

Suborbital shelf absent; lower and posterior suborbitals expanded posteriorly, especially in large specimens, thus covering a large portion of cheek. Basibranchials 1–3 usually each with a pair of large tooth plates. Lower limb of posttemporal not noticeably short or thickened. Postcoracoid process absent. Interpelvic keel well developed; postpelvic process of each side coalesced entire length, not forming an apical fork. Inferior vertebral foramina absent. First anal pterygiophore and haemal spine of first caudal vertebra firmly attached to form a strong strut. Anal pterygiophore expanded anterolaterally to form roof over first two anal spines; first two anal spines articulated proximally with each other; second anal spine asymmetrical, with deep groove on one side of anterior face. Caudal skeleton with 2 epurals and 2 pairs of uroneurals.

Key to Species of *Oligoplites*

1a. Upper jaw 41 to 46 percent HL; body depth 18 to 22 (mean 20.0) percent FL; head length usually equal to or greater than body depth; specimen figure 10a .... *O. refulgens* (Pacific)

1b. Upper jaw 52 to 70 percent HL; body depth 23 to 38 percent FL; head length less than body depth 2

2a. Ventral profile of dentary strongly convex (fig. 9c); premaxillary teeth in a single row, somewhat irregular in young; gillrakers of lower limb of first gill arch 17 to 20 (mean 18.8); first dorsal spines consistently 4; specimen figure 9c .... *O. saliens* (Atlantic)

2b. Ventral profile of dentary moderately convex; premaxilla with 2 distinct rows of teeth or a band of villiform teeth; gillrakers on lower limb of first gill arch 8 to 18 (11 to 15 in Atlantic species); first dorsal spines 4 to 6 3

3a. Upper jaw 52 to 57 (mean 54.7) percent HL; body depth 23 to 28 percent FL; gillrakers on lower limb of first gill arch 13 to 18; premaxillary teeth essentially in 2 distinct rows, an additional row of minute teeth may occur anteriorly; first dorsal spines typically 5; specimen figures 9a and 10b .... *O. saurus* (Atlantic and Pacific)

3b. Upper jaw 58 to 70 percent HL; body depth 24 to 38 percent FL; gillrakers on lower limb of first gill arch 8 to 14; premaxilla with a band of villiform teeth, wide anteriorly; first dorsal spines 4 or 5 4

4a. Top of head with numerous sensory pores, which are connected by network of tubes visible beneath skin; specimen figures 10c, d .... *O. altus* (Pacific)

4b. Sensory pores on top of head sparse, never as numerous as in specimens of *O. altus*; specimen figure 9b .... *O. palometa* (Atlantic)

Oligoplites refulgens Gilbert and Starks.

(Figures 10a, 11, 19; tables 4–5.)

Oligoplites refulgens Gilbert and Starks, 1904, p. 73, pl. 11, fig. 19 (type locality Panama Bay).

This Eastern Pacific species is easily distinguished from its congeners by its short upper jaw and slender body (see table 5). From those species with which it occurs sympatrically, it is also distinguished by its higher number of gill rakers. On the basis of its premaxillary dentition, relationship of predorsal bones to first dorsal pterygiophores, and upper jaw development, it appears to be most closely related to *O. saurus*.

Oligoplites refulgens is the smallest species of the genus, rarely exceeding 250 mm. FL. It occurs in the Gulf of California north at least to Kino Bay, Sonora, Mexico and south to the Gulf of Guayaquil, Ecuador.

Material (61 specimens, 38–230 mm. FL, from 14 collections). GULF OF CALIFORNIA: TABL 103470 (1: 148.5), 103475 (2: 113–131, cleared and stained), 103477 (2: 162), SIO 59–245 (1: 170). GULF OF PANAMA: TABL 103473 (1: 117), 103474 (2: 186–189), 103476 (4: 116–132), 107711 (4: 164–175), USNM 81986 (10 of 36: 38–82). COLOMBIA: TABL 103472 (6: 89–102), 107708 (1: 230). ECUADOR: TABL 103471 (1: 209), TABL 103478 (15 of 38: 115–137). PERU: Zorritos, TABL 107710 (11: 150–196).

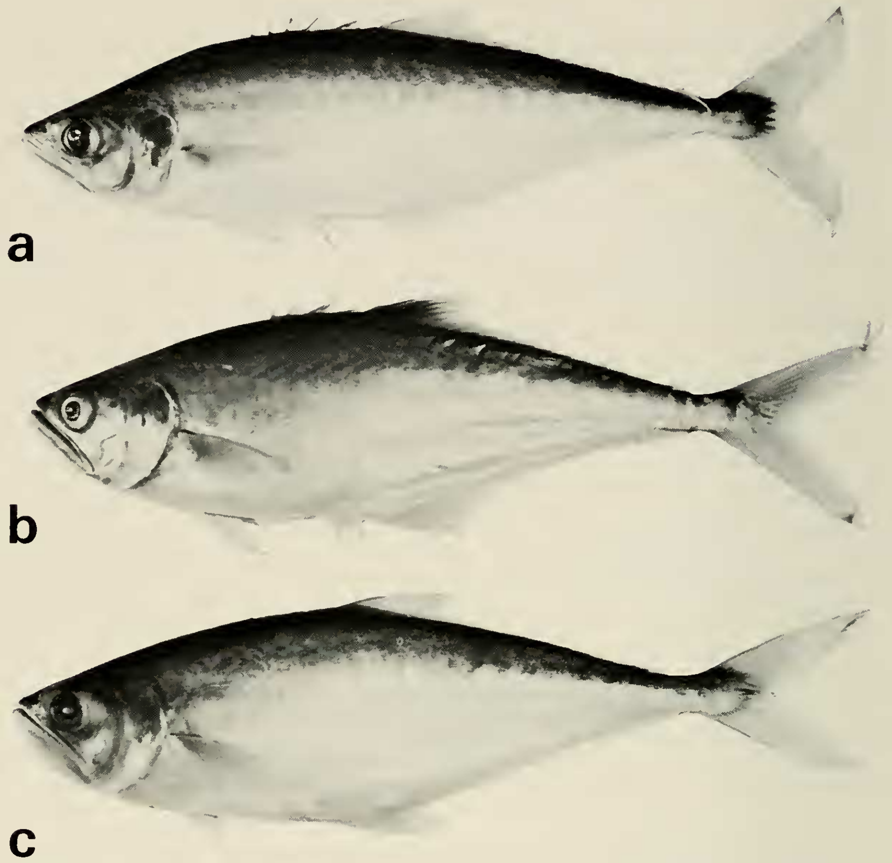


Figure 9. Western Atlantic *Oligoplites*: a, *O. s. saurus*, TABL 101582, 225 mm. FL; b, *O. palometa*, USNM 121804, 245 mm. FL; c, *O. saliens*, TABL 101351, 204 mm. FL.

Oligoplites saliens (Bloch).

(Figures 9c, 11, 14f, 19, 24c; tables 4–5.)

Scomber saliens Bloch, 1793, p. 49, pl. 335 (type locality Antilles).
?*Scomber calcar* Bloch, 1793, p. 55, pl. 336, fig. 2 (type locality Accra, coast of Guinée).
Scomberoides saltator Lacépède, 1802, p. 50 (based on unpublished manuscript of Plumier).

Schultz (1945) did not include *Scomber calcar* in his synonymy of *O. saliens*. Bloch's illustration shows what appears to be a species of *Oligoplites*, with a relatively deep body and 3 first dorsal spines. Since Bloch's description was based on a small specimen, Regan (1903, p. 349) is probably correct in stating that it is "without much doubt, based on a young example of *Scomberoides* [=*Oligoplites*] *saliens*, Bl.". The eastern Atlantic type locality would seem to

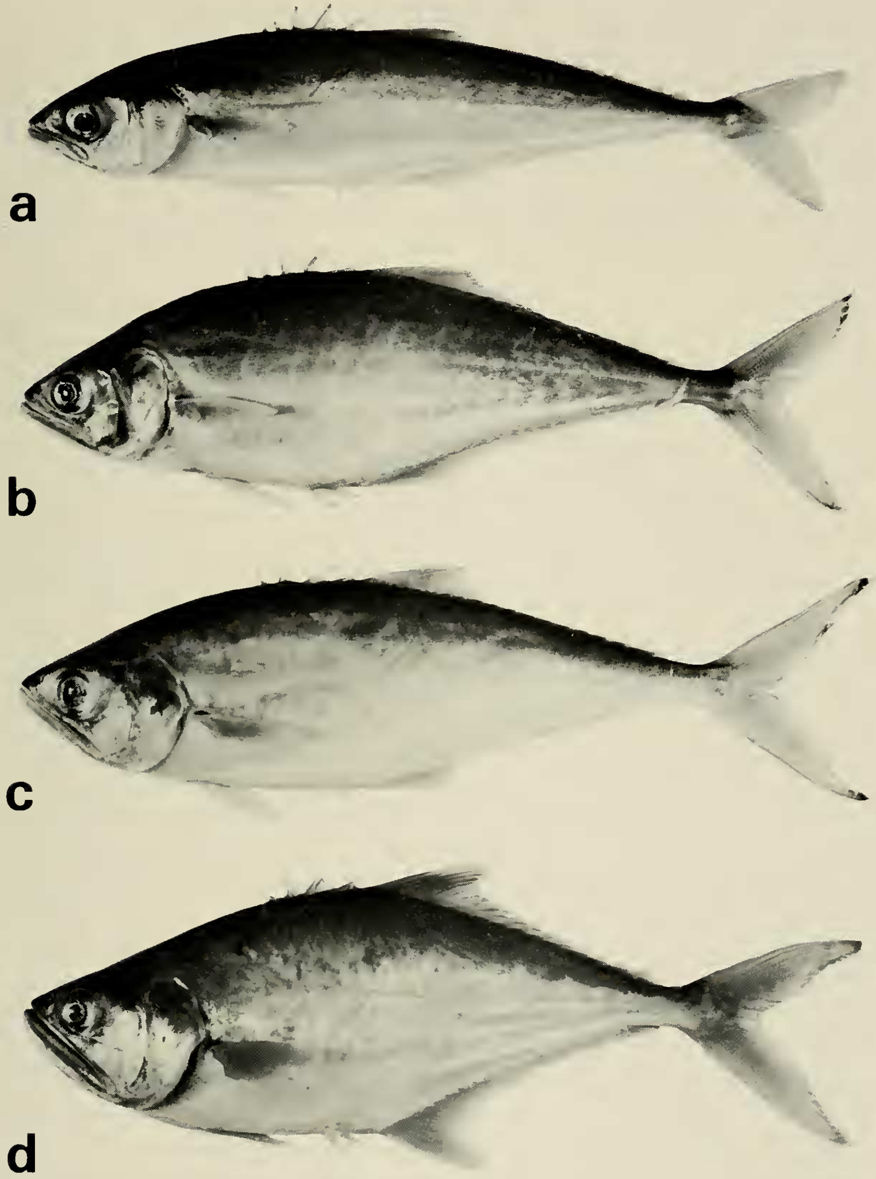


Figure 10. Eastern Pacific *Oligoplites*: a, *O. refulgens*, SIO 59–245, 170 mm. FL; b, *O. saurus inornatus*, TABL 103480, 200 mm. FL; c, *O. altus* UCLA w58-304, 195 mm. FL; d, *O. altus* ('*mundus*' form), UCLA w58-304, 180 mm. FL.

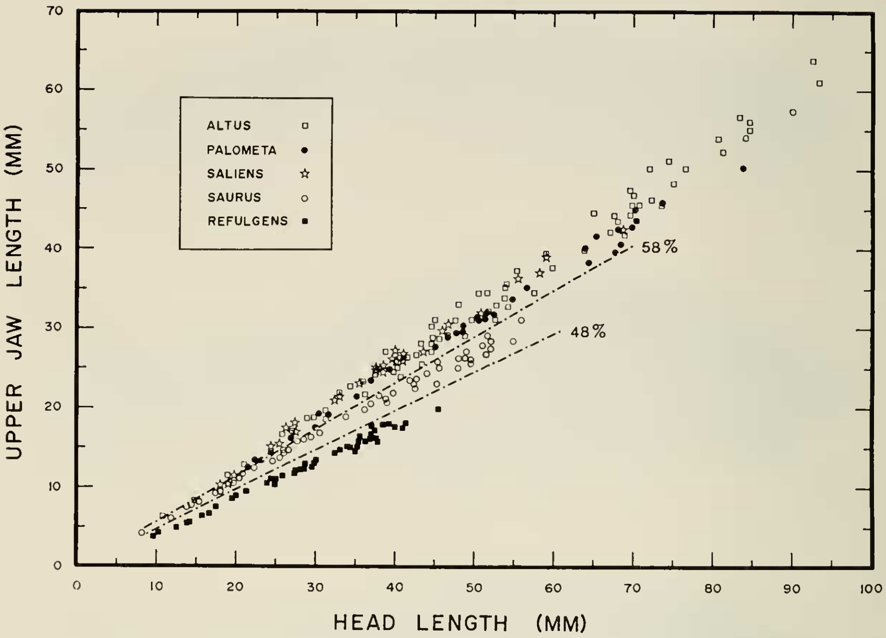


Figure 11. Relationship of upper jaw length to head length in *Oligoplites* species. Dashed lines represent upper jaw length as percent head length.

exclude *S. calcar* representing a species of *Oligoplites,* but the type locality is possibly in error. C. L. Smith has documented a number of such errors (Smith, 1971, pp. 165 and 208) involving other species described by Bloch.

The most diagnostic character of *O. saliens* is the strongly convex ventral profile of its massive lower jaw (see fig. 9c). It is the most specialized species of *Oligoplites* and does not appear to be closely related to any other species. It differs in having a 5 + 4 arrangement of predorsal bones and first dorsal pterygiophores (see table 4), a single row of enlarged premaxillary teeth, and a relatively constant number of outer dentary teeth (see fig. 19) that do not exhibit any recognizable ontogenetic changes. *Oligoplites saliens* can also be distinguished from the other two Atlantic species of *Oligoplites* by its higher number of gillrakers on the lower limb of the first gill arch.

Oligoplites saliens is a large species, attaining at least 390 mm. FL. In the western Atlantic it ranges north at least to Cartasca Lagoon, Honduras, and south to Rio de Janeiro, Brazil.

Material (42 specimens, 88–390 mm. FL, from 25 collections). HONDURAS: Caratasca Lagoon, TABL 101351 (11: 185–219), 101353 (2: 183.5–207), 104795 (5: 195–208). COLOMBIA: UMML 27265 (1: 122). GULF

OF VENEZUELA: TABL 103213 (1: 390), USNM 123073 (1: 88), 123075 (1: 94). TRINIDAD: TABL 104796 (1: 203). GUYANA: TABL 104330 (1: 211), 104378 (1: 235), 107716 (1: 165), 107717 (1: 177). SURINAM: USNM uncataloged *R/V Oregon* station 4175 (1: 169). BRAZIL: Rio Pára, SU 53055 (1: 201), 53062 (1: 249), 53063 (1: 315), 53064 (1: 165); Vitoria, SU 66973 (3[2 cleared and stained]: 95–133), 66975 (1: 146), 66976 (1: 145); Rio de Janeiro, SU 53056 (1: 215), 53057 (1: 270), USNM 76330 (1: 194), 100824 (1: 303), 100825 (1: 295).

Oligoplites saurus (Bloch and Schneider).

(Figures 9a, 10b, 11, 14e, 18, 19, 20c, 21d, 22d; tables 4–5.)

Scomber saurus Bloch and Schneider, 1801, p. 32 (type locality Jamaica).
?*Lichia quiebra* Quoy and Gaimard, 1824, p. 365 (type locality Brazil).
Chorinemus saltans Cuvier *in* Cuvier and Valenciennes, 1831, p. 393 (289) (type locality Martinique).
Chorinemus lanceolatus Girard, 1858, p. 168 (type locality Joseph's Island, Texas).
Chorinemus occidentalis Günther, 1860, p. 475 (type localities Jamaica; San Domingo; Trinidad; Puerto Cabello; Bahia).
Oligoplites inornatus Gill, 1863, p. 166 (type locality west coast of Panama).
Oligoplites rathbuni Miranda-Ribeiro, 1915, p. 8 (type locality Bahia Fish Market, Brazil).

Schultz (1945) apparently overlooked the descriptions of *Chorinemus saltans* and *C. lanceolatus*. The descriptions of both species and their type localities are sufficient to identify them positively as synonyms of *O. saurus*. We have examined the 102 mm. holotype (USNM 710) of *C. lanceolatus*.

Centronotus argenteus Lacépède (1802, p. 316) was questionably included by Schultz in the synonymy of *O. s. saurus*. The name, however, does not appear to be available nomenclaturally, and we regard it as a *nomen nudum*. No description was given and species belonging to two different genera were listed as synonyms.

Oligoplites inornatus was not compared with *O. saurus* in the original description. Despite the fact that these two nominal species were described from different oceans, recent workers have regarded them as only subspecifically distinct at best. The only characters that appear to distinguish them are a slightly higher number of gillrakers and a few more premaxillary teeth anteriorly in Pacific specimens. Certainly the slight differences shown between these two nominal species are not of sufficient magnitude to justify specific separation. However, until large series of specimens from throughout the range of both populations are compared, we believe it is best to maintain them as subspecifically distinct.

The best characters by which to distinguish *O. saurus* are given in the key to *Oligoplites* species. Berry *in* McClane (1965, p. 476) reported that the two detached anal-fin spines of *O. s. inornatus* apparently are connected with toxic glands. In south Florida *O. saurus* is commonly referred to by commercial fishermen as stinging jack. We know of no report of 'stinging' characteristics in any other species of *Oligoplites*.

Although *O. saurus* attains at least 285 mm. FL, it seldom exceeds 250 mm. In the western Atlantic it occurs as far north as the Gulf of Main (Bigelow and Schroeder, 1953, p. 381) and south at least to Recife, Brazil. It is the only species of *Oligoplites* that occurs along the coast of the United States and throughout most of the Caribbean. It has not, however, been reported from the Bahama Islands, perhaps because of the absence of suitable estuarine habitats. In the eastern Pacific *O. saurus inornatus* occurs in the Gulf of California at least to Concepcion Bay, along the outer coast of Baja California to Magdalena Bay, and south to Esmeraldas, Ecuador, and the Galápagos Islands.

Material. The specimens of *O. saurus* which we have studied are listed under the two subspecies as follows:

Oligoplites saurus saurus (71 specimens, 31–285 mm. FL, from 30 collections). GEORGIA: TABL 102643 (1: 191), 103197 (1: 236), 107781 (2: 92–98, cleared and stained). FLORIDA: UMML 39 (1: 67), 3144 (5: 51–93), 4273 (2: 47–139), 4436 (2: 90–92), 5114 (1: 116), 5628 (1: 60), 5975 (1: 73), 9597 (2: 165–185), 13123 (1: 253), 29468 (4: 211–250), TABL 102682 (1: 188), 104730 (9: 101–128), 105386 (3: 196–285), TABL uncataloged station 67–258 (4: 126–168), station 67–280 (3: 131–152). MISSISSIPPI: TABL 102644 (1: 202). LOUISIANA: TABL 102683 (1: 155). TEXAS: USNM 710 (102, holotype of *Chorinemus lanceolatus*). JAMAICA: TABL 101582 (4: 208–225). MARTINIQUE: TABL 103469 (1: 206), 105791 (3: 130–179). GRENADINE ISLAND: TABL 104420 (2: 84–98). TRINIDAD: TABL 103466 (4: 31–144), 104372 (1: 259), 105364 (4: 230–269). VENEZUELA: Carupano, TABL 103207 (3: 199–280). BRAZIL: Recife, SU 51844 (2: 192–196).

Oligoplites saurus inornatus (27 specimens, 53–257 mm. FL from 12 collections). GULF OF CALIFORNIA: TABL 103481 (6: 112–132), 103483 (7: 53–93), SIO 60–298 (2: 110–125), USNM 101037 (1: 246). BAJA CALIFORNIA: Magdalena Bay, SIO-304 (3: 104–109). MEXICO: Banderas Bay, TABL 103479 (1: 220), 103482 (1: 104). COSTA RICA: SIO H52-93 (2: 253–257). PANAMA: USNM 30959 (248, holotype of *Oligoplites inornatus*), TABL 105800 (1: 127). ECUADOR: Esmeraldas, TABL 103480 (1: 200). GALÁPAGOS ISLANDS: AMNH 8308 (2: 71–75).

Oligoplites altus (Günther).

(Figures 10c, 10d, 11; tables 4–6.)

?*Lichia albacora* Guichenot, 1848, p. 231 (type locality Valparaiso, Chile).

Chorinemus altus Günther, 1868, p. 433, unnumbered fig. (of head) (type locality west coast of Panama).

Oligoplites mundus Jordan and Starks *in* Jordan and Evermann, 1898, p. 2844 (type locality San Juan Lagoon, Mexico, mouth of Ahome River).

In the original description *Lichia albacora* was compared only with *Scomber calcar* Bloch, a probable synonym of *Oligoplites saliens.* The description, although poor, applies best to a species of *Oligoplites.* The statement "each jaw has two rows of velvet teeth" is a good description of the teeth in a young individual of *Oligoplites,* but the single type was reported to be 45 inches total length. However the following statements, also given in the description, suggest that the type was small, probably only 4.5 inches TL: "The fishermen of Valparaiso catch it on rare occasions. It seems that it is usually much larger than the one we have observed." *Lichia albacora* may have been based on a young specimen of *O. altus.* This species is known to occur farther south than the other eastern Pacific members of *Oligoplites,* and the first dorsal spine count of three may have been the result of overlooking the small, frequently depressed, first spine. The type of *Lichia albacora* could not be located in the Museum National d'Histoire Naturelle, Paris, where, if extant, it should be deposited.

Schultz (1945) regarded *Oligoplites mundus* as a distinct species, distinguished from *O. altus* on the basis of a slightly longer upper jaw. Both species were otherwise very similar, sharing a number of characters not found in other Pacific species of *Oligoplites.* Schultz had only two examples which he considered conspecific with *O. altus,* the same two specimens on which the account of the species in Meek and Hildebrand (1925, p. 388) is based. We have examined 80 specimens, including the type of *O. mundus* and Schultz's two examples of *O. altus.* However, more specimens are needed before it will be possible to resolve the systematic status of the two forms. Because we are unable to confidently assign a large number of specimens to one or the other form, we tentatively regard them as conspecific.

The species, as here defined, exhibits a more extreme range of variation in several characters than is found in other species of *Oligoplites.* Particularly striking is the range of variation in upper jaw length (see table 6). This variation is not due to sexual dimorphism; nor is it due to population differences, because specimens of approximately the same size, from the same station, exhibit the extremes in variation for several characters. Individuals with long jaws generally have deeper bodies, higher fin lobes, smaller eyes, fewer gillrakers, dorsal spines, and segmented dorsal- and anal-fin rays than do their short jawed counterparts. When any of these characters are plotted against upper jaw length (expressed as percent head length) an obvious negative or positive correlation with jaw length is apparent. It is however, impossible to separate specimens into two groups on the basis of these characters. Both forms are distinguished from their congeners in having the dorsum of the head covered with numerous

Table 6. *Comparison of fork length and upper jaw length (as percent head length) in* Oligoplites altus.

Fork Length Class (mm.)	Upper Jaw Length 58–59.9	60–61.9	62–63.9	64–65.9	66–67.9	68–70	N
100–150	—	1	3	6	—	—	10
151–199	3	5	6	4	1	3	22
200–249	2	1	3	2	3	2	13
250–299	—	1	5	3	2	3	14
300–349	—	2	—	4	1	2	9
350–380	—	—	1	3	1	1	6

sensory pores, which are connected by a network of tubes visible beneath the skin. They may also be distinguished from those species with which they occur sympatrically by their premaxillary dentition, lower number of gillrakers, and longer upper jaw (see table 5). An explanation for the wide range of variation in upper jaw length and strong correlation with several other characters in *O. altus* is a subject that requires investigation by future workers. One possibility that should be considered is that this variation is due to introgressive hybridization (see Anderson, 1949). In many of its characters the short jawed form of *O. altus* is intermediate between the long jawed form and *O. saurus inornatus.*

Oligoplites altus reaches at least 379 mm. FL and attains the greatest body depth of any *Oligoplites* species. On the basis of our material, *O. altus* occurs in the northern Gulf of California, north at least to Punta Estrella, along the outer coast of Baja California to Magdalena Bay, and south to the Gulf of Guayaquil. It has also been reported by several authors from Peru, apparently on the authority of Tortonese (1939, p. 338), who listed a single specimen from Callao.

Material (81 specimens, 27–379 mm. FL, from 36 collections). BAJA CALIFORNIA: Magdalena Bay, TABL 105541 (2: 354–372), 105544 (1: 348), SIO 62–718 (2: 259–299), 62–725 (7 of 11: 281–300). GULF OF CALIFORNIA: TABL uncataloged, Almejas Bay (2: 236–317), TABL 105534 (1: 315), 105542 (1: 355), 105543 (2: 332–354), SIO 61–180 (8: 171–199), 61–182 (1: 257), UCLA W50-46 (2: 195–209), W52-132 (1: 168), W58-48 (2: 147–149). MEXICO: San Juan Lagoon, USNM 48876 (231, holotype of *O. mundus*); Tepic, USNM 130860 (2: 122–137.5); Banderas Bay, TABL uncataloged (2: 112–114). EL SALVADOR: USNM 87338 (1: 72), TABL 104616 (1: 231). COSTA RICA: Gulf of Nicoya, TABL uncataloged (2: 292–314), UCLA W54-12 (1: 130), W54-171 (1: 138.5). GULF OF PANAMA: SIO 58–402 (3: 250–310), UCLA W58-303 (2: 189–212), W58-304 (8: 162–202), W58-305 (3: 137–155), USNM 80063 (1: 198), 82043 (1:215), 128698 (3: 27–59), 128699 (1: 83); San Miguel, TABL uncataloged (3: 178–298). COLOMBIA: Buenaventura Market, TABL uncataloged (1: 241). ECUADOR: Esmeraldas, TABL 105528 (1: 207), 105529 (2: 195–201), TABL uncataloged (1: 220); Gulf of Guayaquil, TABL 107260 (2: 379), TABL uncataloged (6: 222–337).

Oligoplites palometa (Cuvier).

(Figures 9b, 11, 19; tables 4–5.)

Chorinemus palometa Cuvier *in* Cuvier and Valenciennes, 1831, p. 392 (288) (type locality Lake Maracaibo, Venezuela).

?*Chorinemus guaribira* Cuvier *in* Cuvier and Valenciennes, 1831, p. 393 (289) (type locality Brazil).

This western Atlantic species is very closely related to the eastern Pacific *O. altus*. Both species are separable from other forms of *Oligoplites* on the basis of their premaxillary dentition, which consists of a band of villiform teeth along entire length of premaxilla, wide anteriorly, becoming narrow posteriorly. Superficially they are very similar, although *O. altus* is generally a more deep-bodied fish. The only character that will separate these two species is the relative development of cephalic pores. Reduction of cephalic pores in *O. palometa* suggest that it is the more specialized of the two species.

Oligoplites palometa is a large species, attaining at least 392 mm. FL. It occurs from Lake Yzabal, Guatemala, south to São Paulo, Brazil.

Material (42 specimens, 84–392 mm. FL, from 22 collections). GUATEMALA: Lake Yzabal, USNM 13480 (1: 139). NICARAGUA: AMNH 19027 (18: 84.5–160), USNM 44205 (3: 329–268), 45373 (1: 348), 45374 (1: 317), 45375 (1: 304). GULF OF VENEZUELA: USNM 121803 (1: 344), 121804 (1: 245), 121805 (2: 241–303), 121806 (1: 133.5). BRAZIL: USNM 100817 (1: 342), 100847 (1: 392), 100851 (1: 297), SU 66978 (1: 141); Rio Para, SU 53059 (1: 248), 53060 (1: 219), 53061 (1: 222); Salvador (Bahia), SU 53054 (1: 335); Recife, SU 53058 (1: 305), 67028 (1: 334); São Paulo, SU 67007 (1: 171), 67014 (1: 228).

Parona Berg, 1895

Paropsis Jenyns, 1842, p. 65 (type-species: *Paropsis signatus* Jenyns, 1842, by monotypy).

Parona Berg, 1895, p. 39 (substitute name for *Paropsis* Jenyns, 1842, preoccupied, and, therefore, taking the same type species: *Paropsis signatus* Jenyns, 1842).

This monotypic genus is restricted to subtropical and temperate waters of the south Atlantic from Brazil to southern Argentina. Almost nothing has been published on the biology of *Parona*, although the genus is reported (Evermann and Kendall, 1906, p. 99) to be very common along the whole coast of Argentina, and caught at Montevideo, Uruguay, during certain times of the year in enormous quantities. The unusual lateral line with 5–9 dorsal branches, the deep, compressed body, and the lack of pelvic fins suggest that their ecology differs from that of most carangids. Norman (1937, p. 59) reported six specimens, 465–600 mm. SL, caught by otter trawl in 51–56 m.; these specimens are the largest examples known to us. Nothing on the osteology of *Parona* has been published previously.

Description. Body strongly compressed. Adipose eyelids poorly developed. Body, except head, covered with oval-shaped scales. Lateral-line scales not developed into scutes. Lateral line with 5–9 dorsal branches; horizontal portion of lateral line straight except for moderate curve over pectoral fin. Anterior rim of shoulder girdle smooth, without fleshy papillae or deep groove near isthmus. Premaxillae not protractile, connected anteriorly to snout at midline by a narrow fleshy bridge. Swimbladder simple, not bifid posteriorly. Posterior dorsal- and anal-fin rays not consisting of semidetached finlets; ultimate and penultimate rays no more closely spaced than adjoining rays; none of dorsal- or anal-fin rays produced into long filaments. Pelvic fins absent. Pectoral fins short, not falcate, 60.0 to 67.0 percent head length in adults. Upper jaw extending posteriorly from slightly behind (young) to well behind (adult) orbital rim, 52.6 to 57.0 percent head length in adults. Depth (origin D_2 to A_2) 37.4 to 44.0 percent fork length in adults.

Predorsal bones 4; dorsal-fin rays VI-VII (rarely VII) + I, 32 to 37; total dorsal-fin rays 39–44. Anal-fin rays II + I, 34 to 38. Pectoral-fin rays I, 19–21. Pelvic fins absent. Vertebrae 10 + 17 = 27, epipleural ribs 10 or 11. Branchiostegal rays 3 + 6 (epihyal + ceratohyal). Upper gillrakers 4 to 8; lower gillrakers 15 to 17; total gillrakers 20 to 24.

Fronto-supraoccipital crest high; temporal crest extending nearly straight forward to front of the frontal; preorbital region short. Epiotics broadly united along midline of cranium internally. Zygapophyses of exoccipital united beneath foramen magnum. Parasphenoid not expanded into a broad, flattened plate posteriorly. Myodome with broad, posterior opening. Basioccipital without a pair of lateral processes on ventral surface. Ascending process of premaxilla short and triangular; maxilla and premaxilla relatively broad, not closely attached to premaxilla. Premaxillary spur very reduced, consisting of only a slight bulge. Large supramaxilla present. Interosseous space between dorsal arm of dentary and upper margin of articular well developed. Well developed teeth on dentary, premaxilla, palatines, and vomer; dentary and premaxillary teeth conical, arranged in a narrow band anteriorly becoming a single row posteriorly; symphyseal premaxillary and dentary teeth of juveniles slender and caniniform. Mesopterygoids partially covered by a patch of free-floating granular teeth. Pharyngeals not noticeably enlarged, covered with sharp, pointed teeth.

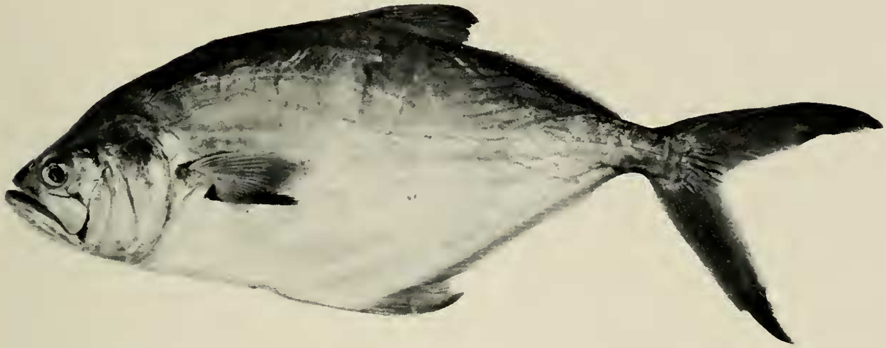


FIGURE 12. *Parona signata*, USNM 87730, 335 mm. FL.

Suborbital shelf present; lower and posterior suborbitals not expanded posteriorly to cover a large portion of cheek. Basibranchials 1–3, each with a large, median tooth plate. Lower limb of posttemporal not noticeably short or thickened. Postcoracoid process well developed. Inter-pelvic keel absent; postpelvic process of each side coalesced entire length, not forming an apical fork. Inferior vertebral foramina absent. First anal pterygiophore and haemal spine of first caudal vertebra firmly attached to form a strong strut. Anal pterygiophore not expanded anterolaterally to form roof over first two anal spines; first two anal spines not articulated proximally with each other; second anal spine symmetrical, without deep groove on one side of anterior face. Caudal skeleton with 2 epurals and 2 pairs of uroneurals.

Parona signata (Jenyns).

(Figures 12, 14a, 15a, 16a, 20a, 21a, 22a, 23a, 24d, 25a.)

Paropsis signatus JENYNS, 1842, p. 66, pl. 13 (type locality Bahia Blanca, coast of northern Patagonia).

DESCRIPTION. Since *Parona* is monotypic, refer to generic description.

PIGMENTATION. Most specimens of *Parona signata* have a conspicuous elongate, horizontal, black blotch on sides beneath pectoral fins, which may also extend onto base of ventral third of pectoral fin. In a few specimens this blotch is short and almost completely hidden by the pectoral fin; it is completely absent in 7 small specimens (TABL 102908) from Argentina. A small round spot at the dorsal origin of the pectoral fin is present on all specimens. Also present on all specimens is a dusky blotch on dorsal third of opercle, heavily pigmented areas, slightly larger than pupil, on either side of snout that are separated at dorsum by paler region, and concentration of pigment at tip of lower jaws. Jenyns (1842, p. 67) reported the life colors as "uniform bright silvery, the ridge of back bluish: a patch of black on the gill-cover, and another under the pectoral fin."

Distribution. Southern Brazil to southern Argentina. Apparently restricted to western Atlantic Ocean. Reported from Chile "Blacino del Rio Santa Cruz" (Fowler, 1945, p. 70), but this record needs verification. The same locality is generally listed as being in Argentina.

Material (20 specimens, 75–368 mm. FL, from 11 collections). BRAZIL: TABL 107713 (2: 358–368); Florianopolis, SU 53052 (1: 264), 53053 (1: 360); Port of Rio Grande do Sul, SU 51868 (2: 171–192). URUGUAY: USNM 87730 (2: 312–335), 86715 (1: 148 mm. SL, cleared and stained); Montevideo, USNM 77375 (1: 135), 86689 (1: 298). ARGENTINA: USNM 53441 (1: 289); Buenos Aires, TABL 101156 (1: 270); Mar del Plata, TABL 102908 (7: 75–84, 3 cleared and stained).

Hypacanthus Rafinesque, 1810

Hypacanthus Rafinesque, 1810, p. 43 (type-species: *Centronotus vadigo* Lacépède, 1802 = *Scomber amia* Linnaeus, 1758, by present designation).

Lichia Cuvier, 1817, p. 321 (type-species: *Scomber amia* Linnaeus, 1758, by monotypy).

Porthmeus Valenciennes *in* Cuvier and Valenciennes, 1833, p. 255 (190) (type-species: *Porthmeus argenteus* Valenciennes, 1833, by original designation).

This monotypic genus is restricted to subtropical and temperate waters of the Mediterranean, eastern Atlantic, and southern Indian Ocean. The habitat of *Hypacanthus* is littoral (Poll, 1954, p. 160) ". . . judging by the origins of specimens—collections and total absence of this species from catches of trawls." Along the west African Gold Coast small specimens of *Hypacanthus* are caught in seines, but uncommonly, and they are taken with lines from January to April (Norman and Irvine, 1947, p. 144). Smith (1949, p. 222) states that it "grows to at least 6 feet and is one of the finest game fishes, fighting fiercely to the end; prefers live or moving bait, enters estuaries, and may often be seen in pursuit of mullet on the surface." Superficially *Hypacanthus* most closely resembles *Scomberoides* but differs in having scaled cheeks and a lateral line that is very irregular and sinuous, dropping below midline of body between pelvic fins and origin of anal fin. Nothing on the osteology of *Hypacanthus* has been published previously.

Nomenclature. In his paper on the nomenclature of the European fishes of the subfamily Trachinotinae, Wheeler (1963) clearly demonstrated that *Hypacanthus* is a senior synonym of *Lichia* but chose to regard the older name as a *nomen oblitum* and advocated suppression of the name. We do not believe that this action is justified and continue to recognize *Hypacanthus*. In so doing we have taken special note of the fact that the name *Hypacanthus* has always been correctly applied, while fishes belonging to at least four different carangid genera have been described as new species of *Lichia*.

In the generic diagnosis of *Hypacanthus,* Rafinesque referred to only two species. One of these species, *Centronotus vadigo* Lacépède, is clearly a synonym of *Scomber amia* Linnaeus and is here designated the type-species of *Hypacanthus.* The other reference was to "*Scomber aculeatus* di Linnaeus." As noted by Wheeler (1963, p. 535), the species does not seem to exist in Linnaeus's works and it might be argued that Rafinesque wrote "di Linnaeus" in error for *S. aculeatus* Bloch (1793). Bloch's illustration strongly suggests a species of *Oligoplites* or *Scomberoides,* and several workers have followed Cuvier and Valenciennes (1831, p. 384) in questionably regarding *S. aculeatus* Bloch as a species of *Chorinemus* (=*Scomberoides*). We concur with Wheeler (1963, p. 537) that it is a junior synonym of *Hypacanthus amia* (Linnaeus). Bloch's illustration shows a fish with 7 first dorsal spines (which does not agree with *Oligoplites*), and the species is reported from the Mediterranean where neither *Oligoplites* or *Scomberoides* occurs.

The illustration of *Porthmeus argenteus* Valenciennes (see fig. 13) is unmistakably based on a young individual of *Hypacanthus amia.*

Description. Body moderately to strongly compressed. Adipose eyelids developed. Body, including cheeks, covered with narrow, oval-shaped embedded scales, becoming needlelike on breast. Lateral-line scales not developed into scutes. Lateral line without side branches, very irregular and sinuous, dropping below midline of body between pelvic fins and origin of anal fin. Anterior rim of shoulder girdle smooth, without fleshy papillae or deep groove near isthmus. Premaxillae protractile, separated anteriorly from snout at midline by a complete groove. Swimbladder moderately bifid (in adults), bifurcated portion of swimbladder extending posteriorly to beneath caudal vertebra 6 or 7. Posterior dorsal- and anal-fin rays not consisting of semidetached finlets; ultimate and penultimate rays no more closely spaced than adjoining rays; none of dorsal- or anal-fin rays produced into long filments. Pelvic fins relatively short, not depressible into shallow abdominal groove. Pectoral fins short, not falcate, 51.2 to 63.4 percent head length. Maxilla extends posteriorly to slightly behind orbital rim, 50.5 to 54.2 percent head length. Body depth (origin D_2 to A_2) 31.0 to 39.4 percent fork length.

Predorsal bones 3; dorsal fin rays VII + I, 19–21; total dorsal rays 27–29. Anal-fin rays II-I, 17–20. Pectoral-fin rays I, 18–20. Pelvic-fin rays I, 5. Vertebrae 10 + 14 = 24; epipleural ribs 10 or 11. Branchiostegal rays 2½ + 5½ (epihyal + ceratohyal). Upper gillrakers 1 or 2; lower gillrakers 8 or 9; total gillrakers 9 to 11.

Fronto-supraoccipital crest low; temporal crest poorly developed, not extending forward to posterior rim of orbit and not reaching edge of cranium; preorbital region short. Epiotics not united along midline of cranium internally. Zygapophyses of exoccipital united beneath foramen magnum. Parasphenoid not expanded into a broad, flattened plate posteriorly. Myodome with broad, posterior opening. Basioccipital without a pair of lateral processes on ventral surface. Ascending process of premaxilla short and triangular; maxilla moderately slender, not closely applied to premaxilla. Premaxillary spur absent. Small supramaxilla present. Interosseous space between dorsal arm of dentary and upper margin of articular moderate. Well developed teeth on dentary, premaxilla, palatines, and vomer; dentary and premaxillary teeth slender and pointed, arranged in a broad band anteriorly becoming narrower posteriorly; juveniles without symphyseal premaxillary and dentary canines. Mesopterygoids edentate. Pharyngeals not noticeably enlarged, covered with sharp, pointed teeth.

Suborbital shelf present; lower and posterior suborbitals not expanded posteriorly so as to cover a large portion of cheek. First basibranchial without tooth plates, basibranchials 2–3 each with a pair of small widely separated tooth plates. Lower limb of posttemporal not noticeably short or thickened. Postcoracoid process moderate. Interpelvic keel well developed; postpelvic process on each side not coalesced entire length, forming an apical fork. Inferior vertebral foramina present. First anal pterygiophore and haemal spine of first caudal vertebra firmly attached to form a strong strut. Anal pterygiophore not expanded anterolaterally to form roof over first two anal spines; first two anal spines not articulated proximally with each other; second anal spine slightly asymmetrical, with shallow depression on one side of anterior face. Caudal skeleton with 3 epurals and two pairs of uroneurals.

Hypacanthus amia (Linnaeus).

(Figures 13, 14b, 21b, 22b, 24a.)

Scomber amia LINNAEUS, 1758, p. 299 (based solely on references to Artedi, 1738).

Scomber aculeatus BLOCH, 1793, p. 51, pl. 336, fig. 1 (type locality: no specific locality given; reported from coast of Mediterranean and several localities in Caribbean).

Centronotus vadigo LACÉPÈDE, 1802, p. 318 (type locality Mediterranean).

Porthmeus argenteus VALENCIENNES *in* Cuvier and Valenciennes, 1833, p. 256 (191), pl. 264 (type locality Cape of Good Hope).

NOMENCLATURE. Wheeler (1963, pp. 536–7) gives a detailed discussion of the specific synonymy of *Hypacanthus*. Some additional comments are given in the preceding generic account.

DESCRIPTION. Since *Hypacanthus* is monotypic, refer to generic description.

PIGMENTATION. The young, to at least 120 mm. FL, have prominent vertical bands (fig. 13). Judging from a color illustration of a 2½ inch specimen (Smith, 1949, pl. 25, fig. 539), the bands are brownish-black and the background coloration is yellow-orange. Adults are brown dorsally, silvery white below the lateral line, and have pale brown fins.

DISTRIBUTION. Mediterranean, eastern Atlantic, and Indian Ocean north

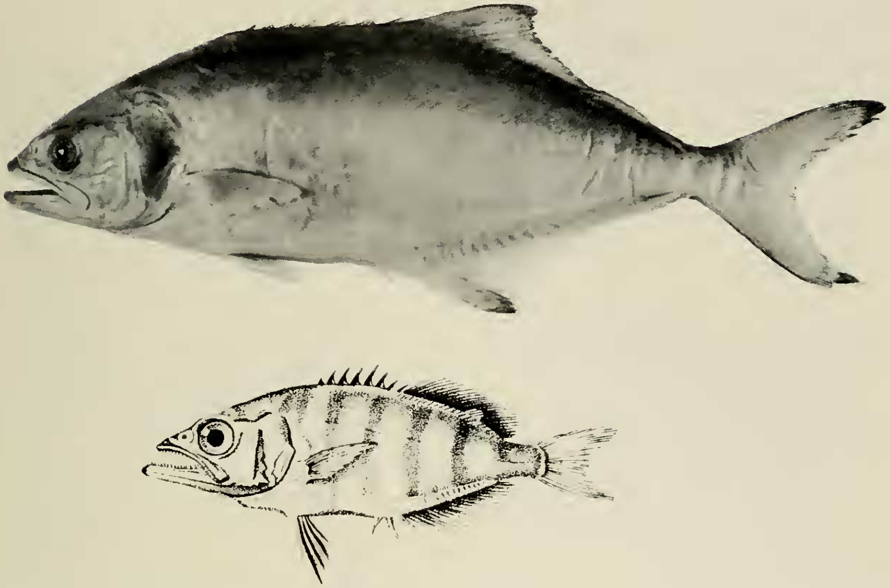


Figure 13. *Hypacanthus amia*: above, TABL 104703, young adult, 200 mm. FL; below, drawing of holotype of *Porthmeus argenteus* = juvenile *H. amia* (after Cuvier and Valenciennes, 1833, pl. 264).

to Delago Bay, Mozambique. The littoral habitat, general occurrence in subtropical and temperate waters and absence of *Hypacanthus* from most of the Indian Ocean indicates that the Indian Ocean distribution of *Hypacanthus* is the result of migration around the Cape of Good Hope.

Material (24 specimens, 62–202 mm. FL, from 5 collections). MEDITERRANEAN: Lebanon, St. George Bay, TABL 104703 (5: 62–200, 1 cleared and stained), 104714 (15 of 30: 79–110, 2 cleared and stained). LIBERIA: Mesurado River, USNM 193783 (1: 202), 193813 (1: 82). SOUTH AFRICA: Durban Harbor, TABL 107250 (2: 190).

Relationships and Zoogeography

Genera *Scomberoides* and *Oligoplites*.

The strong external resemblance and large number of characters shared by *Scomberoides* and *Oligoplites* clearly reflect their intimate relationship, and they are usually placed together in their own subfamily—the Scomberoidinae (=Chorineminae). Some of the more notable shared characters are the following: scales lanceolate or needlelike (fig. 3); the posterior segmented dorsal- and anal-fin rays consisting of semi-detached finlets; two distinct types of dentary

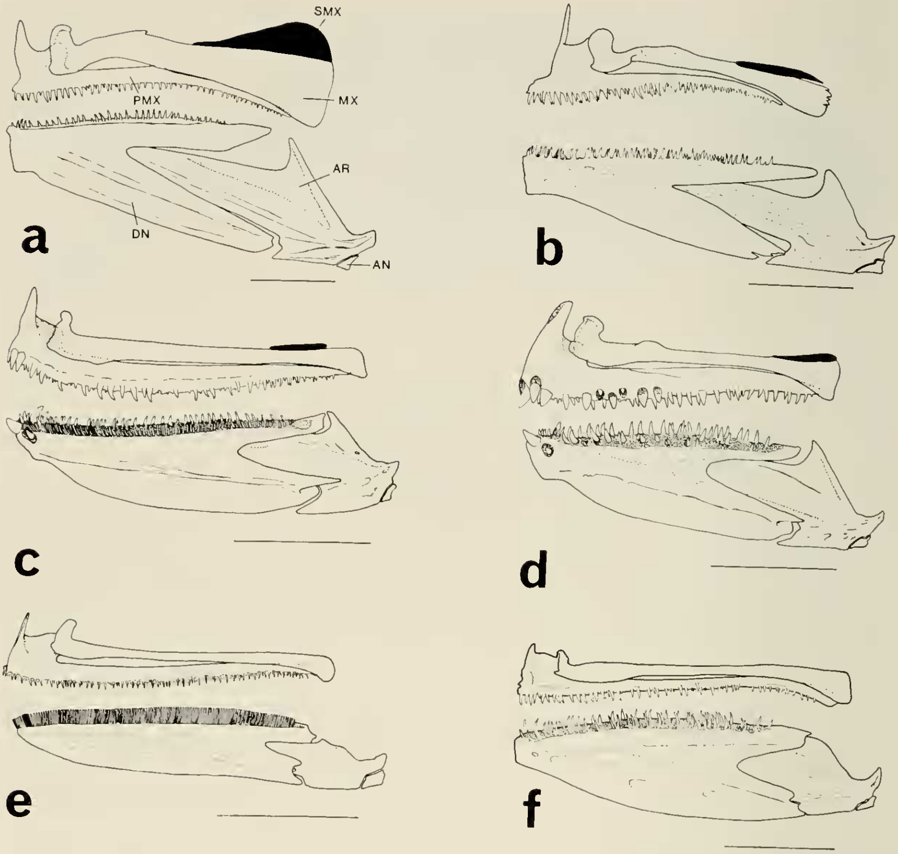


FIGURE 14. Jaw bones: a, *Parona signata*, USNM 86715, 148 mm. SL; b, *Hypacanthus amia*, TABL 104714, 100 mm. SL, c, *Scomberoides commersonianus*, GVF 2195, 86 mm. SL; d, *S. tol*, TABL uncataloged S-V 69–128, 107 mm. SL; e, *Oligoplites s. saurus*, TABL 107781, 91.5 mm. SL; f, *O. saliens*, SU 66973, 122 mm. SL. DN, dentary; AR, articular; AN, angular; PMX, premaxilla; MX, maxilla; SMX, supramaxilla. Scale 5.0 mm.

teeth during different stages of their ontogeny (see discussion below); slender, nearly straight maxillae that are closely applied to the premaxillae; a broad premaxillary frenum; interosseous space between dorsal arm of dentary and upper margin of articular minute or absent (fig. 14); the first anal pterygiophore expanded anterolaterally, forming a roof over anal spines (fig. 15b); the first two anal spines articulated proximally with each other, and the second anal spine asymmetrical with a deep groove on one side of anterior face, so that when anal spines are depressed the first spine folds into the groove in scissor-like fashion; caudal skeleton with 2 epurals (fig. 16b); swimbladder strongly

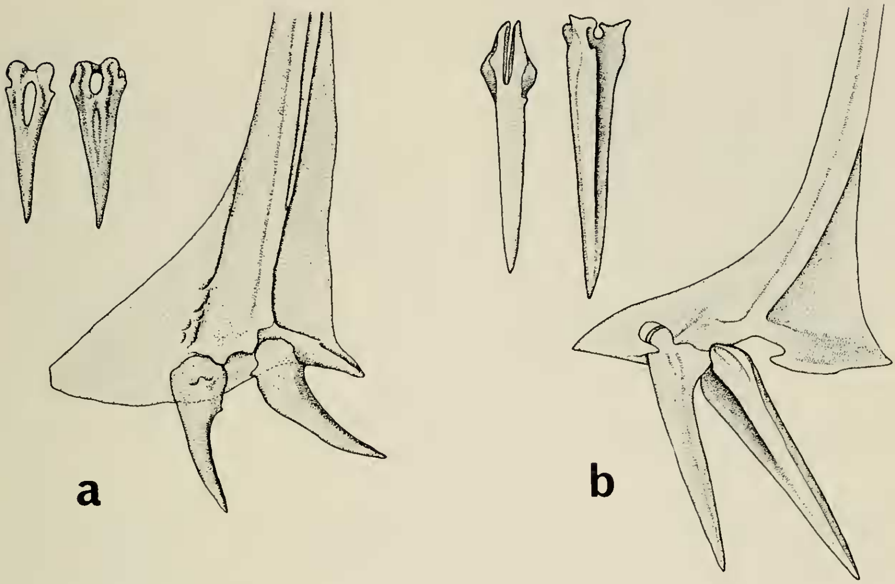


Figure 15. First anal pterygiophore: a, *Parona signata*, TABL 102908, 80 mm. SL; b, *Scomberoides tala*, TABL S-V 69–156, 109 mm. SL.

bifid, even in smallest specimens (fig. 17). All of these conditions probably represent specializations.

Each dentary has two rows of teeth in *Scomberoides* and *Oligoplites*. In most species (exceptions are *S. tol* and *O. saliens*) the outer dentary teeth of juveniles and young adults have spatulate tips, and are closely spaced and strongly hooked outward (fig. 18). This arrangement produces a trough between the inner and outer rows of teeth into which the premaxillary teeth fit when the mouth is closed. In adults these outer 'juvenile teeth' are shed and replaced with more robust, wider spaced teeth that are not strongly hooked and have pointed tips (figs. 18–19). The inner dentary teeth, consisting of a single type, apparently are permanent. We know of no other carangid genus in which there are two distinct types of dentary teeth associated with ontogeny. Since this unusual adaptive feature is shared by both *Scomberoides* and *Oligoplites*, we believe the character was possessed by the progenitor of both genera and its loss in *S. tol* and *O. saliens* must be interpreted as a subsequent specialization. Major (1973) has correlated this change in dentition in *Scomberoides lysan*, *Oligoplites refulgens*, and *O. saurus inornatus* with a shift in feeding habits. Juveniles and young feed primarily on larval crustaceans, and on scales and epidermis of schooling fishes. He suggested that the outer spatulate dentary teeth are inserted under the scales, which are then ripped off. With growth and loss of 'juvenile'

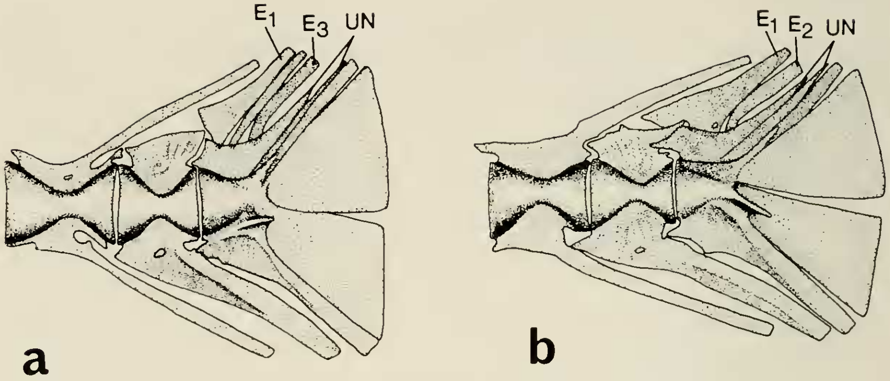


FIGURE 16. Caudal skeleton: a, *Parona signata*, USNM 86715, 148 mm. SL; b, *Scomberoides commersonianus*, GVF 2195, 86 mm. SL. E, epural; UN, uroneural.

teeth there is a gradual shift in diet until these species become fully piscivorous, ingesting whole fish. In juveniles of all species of *Scomberoides* except *S. lysan* the symphyseal dentary and premaxillary teeth are robust and caninelike (figs. 14c–d). Such teeth are greatly reduced or absent in the adults; they are never present in *Oligoplites*.

Carr and Adams (1972) found that ectoparasites, primarily caligoid co-

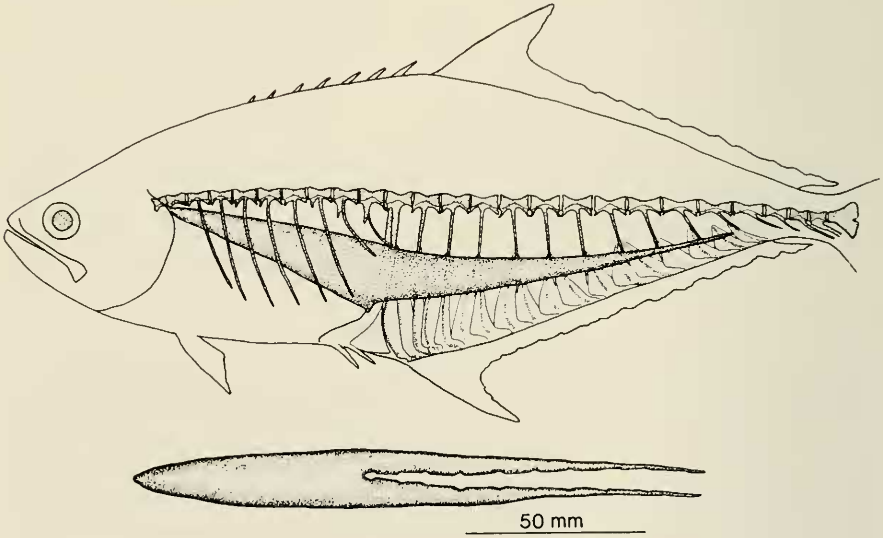


FIGURE 17. Lateral and ventral view of swimbladder of *Scomberoides tala*, TABL 107712, 264 mm. FL.

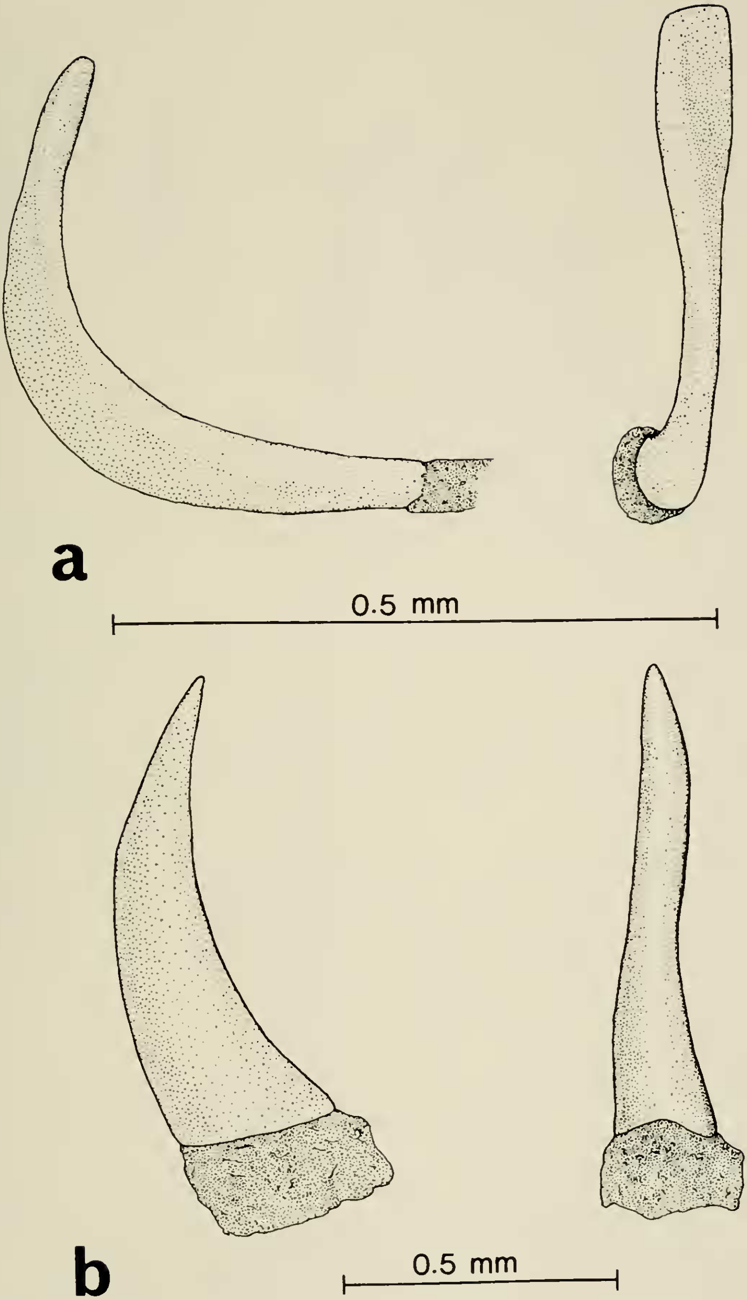


Figure 18. Lateral and frontal view of outer row, dentary tooth of *Oligoplites s. saurus*: a, juvenile 90 mm. FL; b, adult 185 mm. FL.

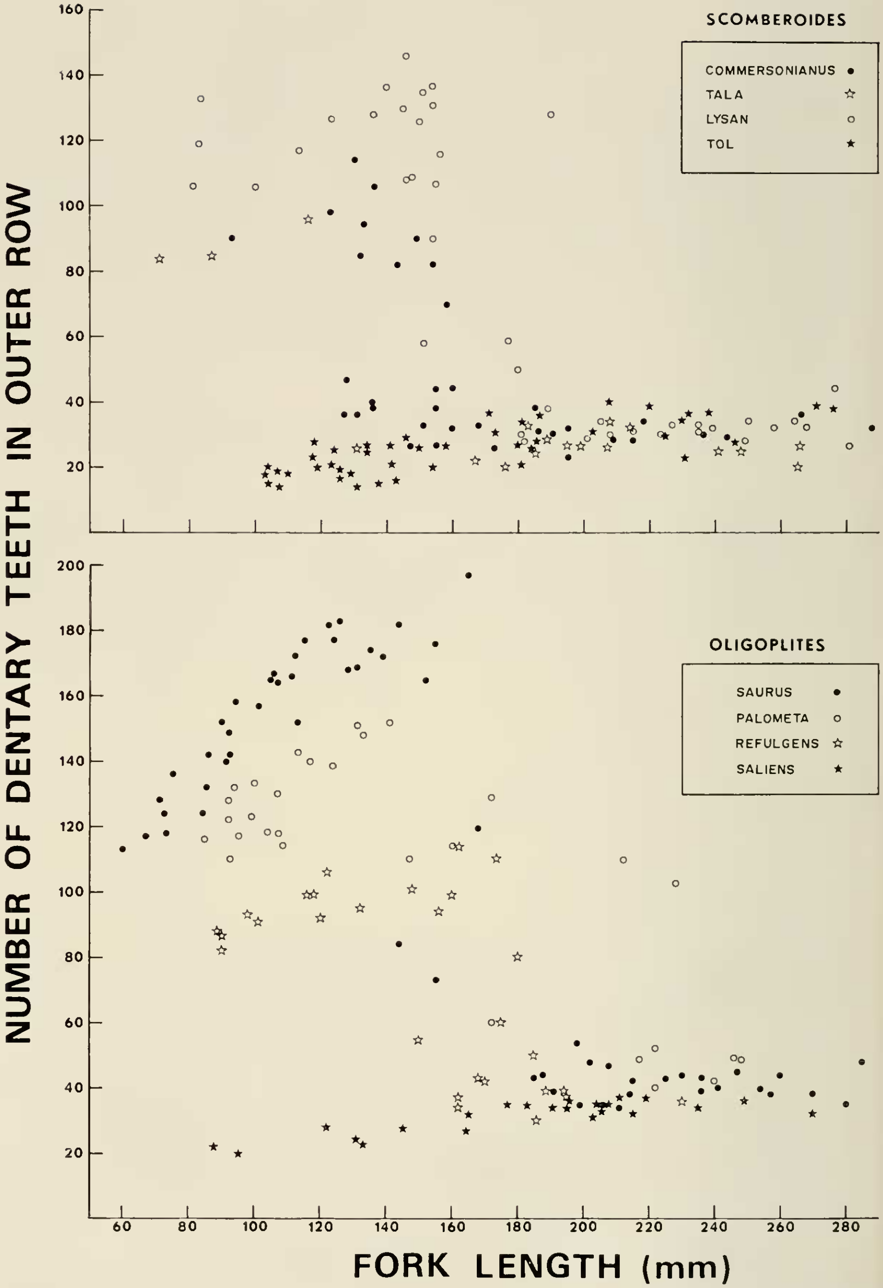


Figure 19. Scatter diagram of outer row teeth on dentary (one side) plotted against fork length for species of *Scomberoides* and *Oligoplites* (*O. altus* and eastern Pacific specimens of *O. saurus* were not plotted).

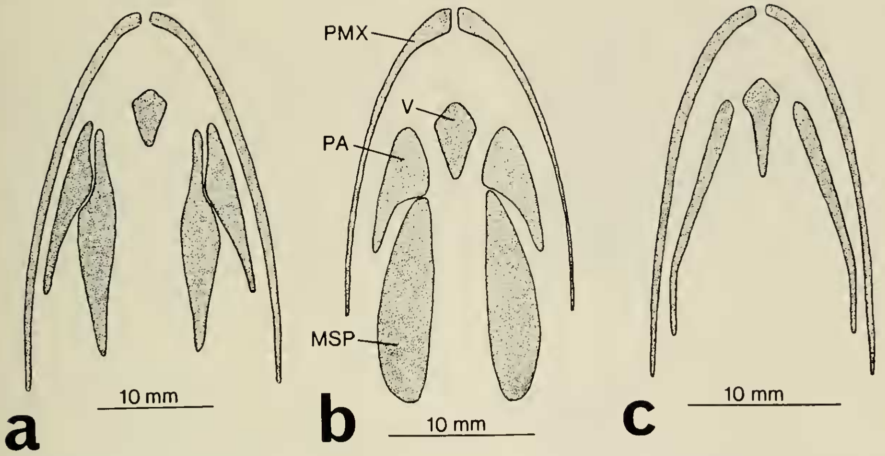


Figure 20. Upper dentition: a, *Parona signata*, TABL 101156, 271 mm. FL; b, *Scomberoides tol*, TABL 107707, 284 mm. FL; c, *Oligoplites s. saurus*, TABL 105364, 230 mm. FL. PMX, premaxilla; V, vomer; PA, palatine; MSP, mesopterygoid.

pepods, accounted for approximately 50 percent of the stomach contents of juveniles of *Oligoplites s. saurus* 26 to 40 mm. SL. In contrast, ectoparasites constituted only 2 to 4 percent of the stomach contents in fish less than 26 mm. or greater than 60 mm. SL. Although no feeding observations were made, they postulated that this carangid passes through a stage in its development in which intentional removal of ectoparasites from other fishes is an important activity. Most of the fish skin, flesh, and scales found in the stomachs of juveniles was presumed to have come from cleaning activities. Major (1973) believed that scales and/or epidermal tissue was the primary food source sought by juveniles of *Scomberoides lysan* in Hawaii. His analysis of the stomach contents of *Oligoplites* juveniles is inconclusive, since the smallest specimen examined was 48 mm. SL. If the conclusions regarding the primary food source sought by juveniles of *Oligoplites* and *Scomberoides* are valid, they may provide valuable insight into the evolution of cleaning symbiosis in fishes. Ectoparasite removal seems to be a more specialized type of feeding than is aggressive scale ingestion, although one that might easily have evolved from the latter activity.

The following characters of *Oligoplites* are interpreted as specializations of the condition found in *Scomberoides* and suggest that the amphi-American endemic distribution of *Oligoplites* is a relatively recent evolutionary development (this does not necessarily imply that the genus evolved elsewhere): 1) reduced number of dorsal spines with a concomitant increase in number of predorsal bones (see discussion under Characters and Methods Section); 2) loss of mesopterygoid teeth (fig. 20c); 3) loss of supramaxilla; 4) loss of suborbital

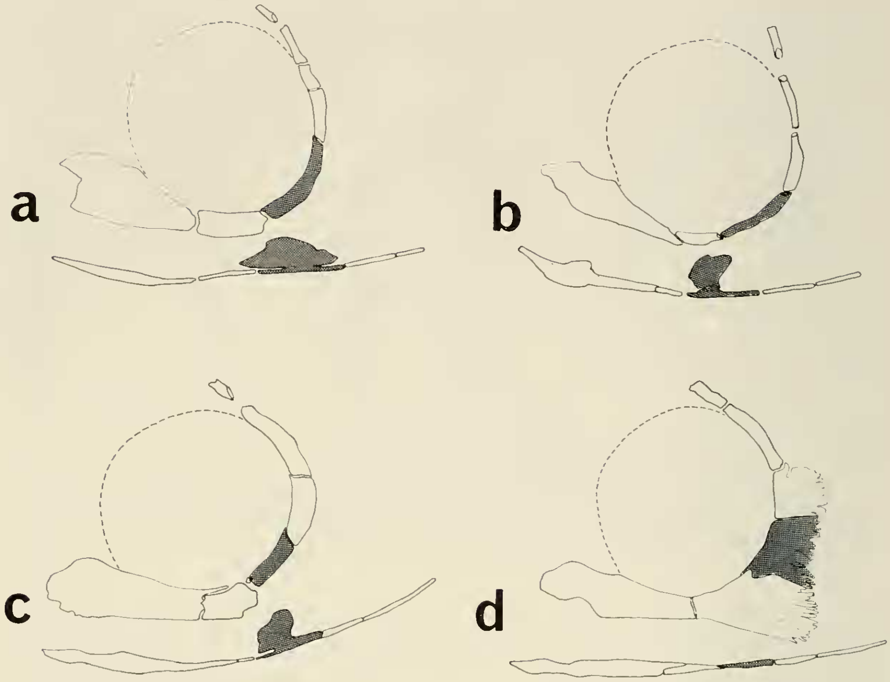


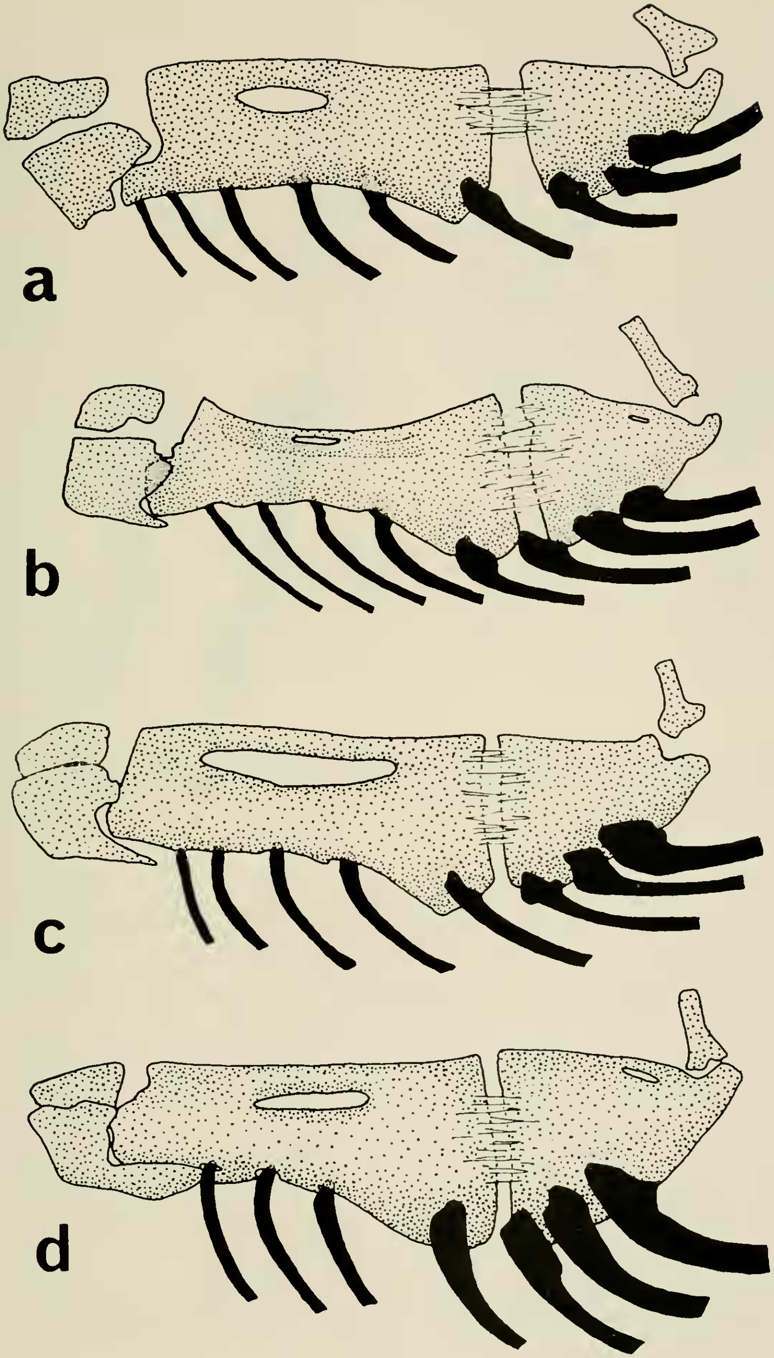
Figure 21. Lateral and dorsal view of suborbital bones: a, *Parona signata* TABL 102908, 83 mm. SL; b, *Hypacanthus amia*, TABL 104714, 100 mm. SL; c, *Scomberoides tol*, TABL S-V 69–128, 122 mm. SL; d, *Oligoplites s. saurus*, TABL 107781, 91.5 mm. SL. Third suborbital bone shaded.

shelf (Smith and Bailey, 1962) and expansion of suborbitals 2–4 posteriorly across cheek (fig. 21d), a character best developed in large specimens; 5) reduction in number of branchiostegal rays (fig. 22d); and 6) presence of needlelike scales in all species. Steps in the evolution from broadly lanceolate to needlelike scales can be seen in figure 3.

We believe that *Oligoplites* evolved from a *Scomberoides*-like ancestor that reached the New World via the Pacific. Although the East Pacific Barrier restricts the distributions of many groups of tropical shorefishes (Briggs, 1961), it is not such a formidable obstacle to carangids as evidenced by the relatively

→

Figure 22. Left hyoid arch; branchiostegal rays shown in black: a, *Parona signata*, USNM 86715, 148 mm. SL; b, *Hypacanthus amia*, TABL 104714, 100 mm. SL; c, *Scomberoides tol*, TABL S-V 69–128, 122 mm. SL; d, *Oligoplites s. saurus*, TABL 107781, 91.5 mm. SL.


a
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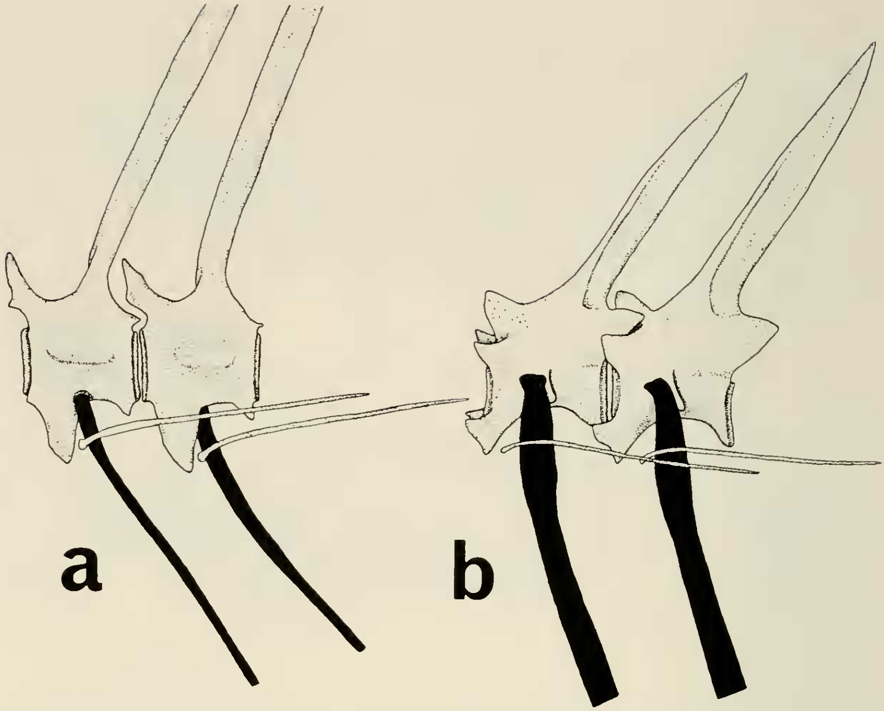

FIGURE 23. Fifth and sixth precaudal vertebrae (pleural ribs are shown in black): a, *Parona signata*, TABL 102908, 80 mm. SL; b, *Scomberoides commersonianus*, GVF 2195, 86 mm. SL.

large number of circumtropical genera and species. One widely distributed Indo-West Pacific carangid, *Caranx* (*Gnathanodon*) *speciosus* (Forskål), that has become established in the eastern Pacific appears to be a recent migrant across this several thousand mile stretch of open ocean. The wide distribution of *Scomberoides lysan* in the central Pacific demonstrates that this group of carangids also has the ability to cross large stretches of oceanic water. Given this potential, it is not difficult to envision successful bridging of the East Pacific Barrier by a *Scomberoides*-like carangid. As previously noted, the nature of the characters that differentiate *Oligoplites* from *Scomberoides* indicates a relatively recent evolutionary separation. This suggests that by the time the progenitor of *Oligoplites* reached the new world it possessed most of the characters present in *Scomberoides*.

Although inconclusive, the known fossil carangid record supports the above hypothesis. Middle Eocene deposits from Monte Bolca near Verona, Italy contain a fairly rich carangid fauna (Blot, 1969) but no *Oligoplites*-like fossil has

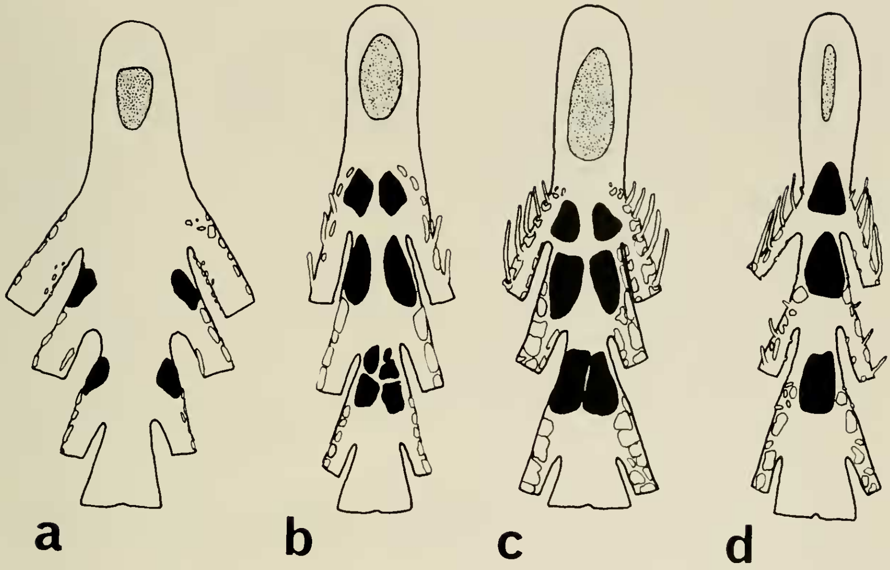

Figure 24. Basibranchial tooth plates (shown in black) and basihyal teeth (stippled): a, *Hypacanthus amia*, TABL 104714, 100 mm. SL; b, *Scomberoides tala*, TABL S-V 69-156, 109 mm. SL; c, *Oligoplites saliens*, SU 66973, 122 mm. SL; d, *Parona signata*, TABL 102908, 80 mm. SL.

been found. The only record of a fossil *Oligoplites* outside the new world appears to have been based on a misidentification (see discussion of *Scomberoides spinosus*).

Genus *Parona*.

Parona parallels *Scomberoides* (and *Oligoplites*) in several of its specialized characters, has others not found elsewhere in the Carangidae, and shares with *Hypacanthus* and *Trachinotus* a number of generalized (primitive) characters that have become specialized in the Scomberoidinae. Characters that suggest affinity with *Scomberoides* are the broadly united epiotics, high number of caudal vertebrae, fusion of the basibranchial tooth plates and presence of a premaxillary frenum. In having the epiotics broadly united internally, *Parona* possesses a character utilized by Starks (1911) and Suzuki (1962) in defining the subfamily Scomberoidinae. The shape of the precaudal vertebrae and the position of attachment of the pleural ribs is very different from the condition in *Scomberoides* (fig. 23). This is probably due to differences in body shape however, because *Parona* and *Trachinotus ovatus* (Linnaeus), which have considerably deeper bodies than do the species of *Scomberoides*, have precaudal vertebrae that are nearly identical.

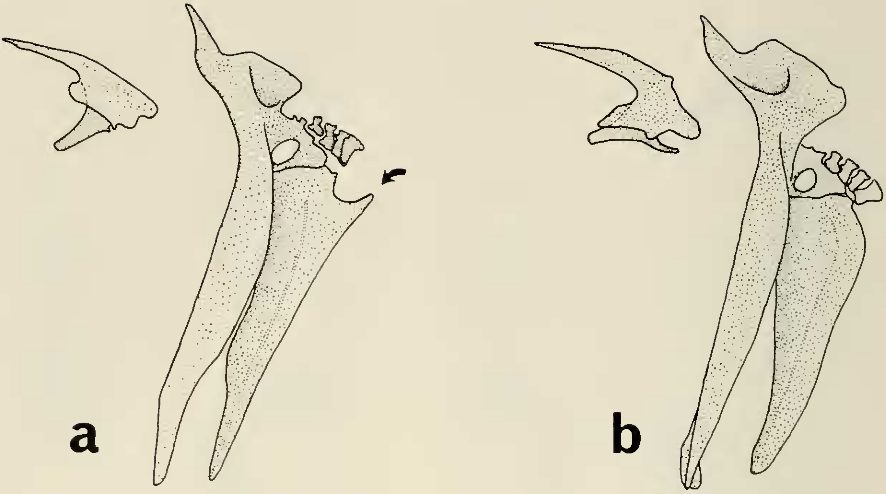

FIGURE 25. Posttemporal, clavicle, hypercoracoid, hypocoracoid, and radials (arrow points to postcoracoid process): a, *Parona signata*, TABL 102908, 80 mm. SL; b, *Scomberoides commersonianus*, GVF 2195, 86 mm. SL.

Nelson (1969, p. 500) noted that there are three pairs of basibranchial tooth plates in *Chorinemus*, and the median plates of *Parona* (fig. 24d) must have arisen through fusion of such paired elements (his "*Chorinemus occidentalis*" = *Oligoplites s. saurus*). He also stated (p. 502) that "jaw protrusion and pharyngeal-bone mobility seem to be improvements, and shearing and grinding jaw dentitions are specializations, inversely correlated with basibranchial dentition. The large paired plates (and their median derivatives, e.g., in *Parona*) that in some cases occur over the basibranchials of teleosts could represent a reversal in the general trend toward loss of basibranchial dentition. Functionally, this reversal would mean that the basibranchial area in some cases is secondarily involved in seizing and holding large prey." Since the species of *Parona*, *Scomberoides*, and *Oligoplites* have the best developed basibranchial dentition in the family, comprise the only carangid genera that have a premaxillary frenum (which restricts upper jaw protrusability), and feed on large prey as adults, we believe that the well developed basibranchial plates of these genera represent a secondary specialization associated with mode of feeding.

The mutual occurrence in these genera of several derived character states that are not found in any other carangids is here interpreted as evidence that *Parona* and *Scomberoides* evolved from a common ancestor. Although some of the shared specializations, especially those associated with trophic ecology, might be due to parallelism, this does not seem likely in the case of united epiotics.

Parona differs from all other carangids in having typically 9 branchiostegal rays and in lacking pelvic fins (a small pelvic girdle is retained). The pelvic fins are very reduced, however, in *Trachinotus stilbe* (Jordan and McGregor), and in fossil trachinotid genus *Paratrachinotus* (Blot, 1969, p. 285). The lateral line of *Parona* is unusual in having 5–9 dorsal branches. The mesopterygoid teeth are firmly ankylosed to the mesopterygoid in *Scomberoides*. In *Parona* the 'mesopterygoid' teeth are free-floating and thus may not be homologous. The first anal pterygiophore and articulation of the first two anal spines is very generalized compared to the complex arrangement in *Scomberoides*. Other generalized characters of *Parona* are the relatively broad, curved maxillae; well developed interosseous space between dorsal arm of dentary and upper margin of articular; large supramaxillae; caudal skeleton with 3 epurals; and broad, oval-shaped scales. The shoulder girdle of *Parona* differs from that of all other carangids, except those of the subfamily Naucratinae, in having a well developed postcoracoid process (fig. 25a).

The large number of differences between *Parona* and *Scomberoides* suggest that they have had a long history of evolutionary separation. The restriction of *Parona* to subtropical and temperate waters of the South Atlantic Ocean probably reflects an extended period of isolation in that region.

Genus *Hypacanthus*.

Hypacanthus differs from the previous genera in having inferior vertebral foramina; post-pelvic processes forming an apical fork; the lateral line very irregular and sinuous, dropping below the midline of body between the pelvics and origin of anal fin; poorly developed basibranchial dentition; young with strong vertical bars (young of the other genera lack such bars); and completely scaled cheeks. The most notable thing about *Hypacanthus* is the lack of any obvious specialized characters (except perhaps the lateral line). The eastern Atlantic-Mediterranean distribution of *Hypacanthus* and its general occurrence in subtropical and temperate waters supports the hypothesis that it evolved in the Mediterranean region.

The exact phyletic position of *Hypacanthus* is obscure owing to the lack of specialized characters which might be useful in determining relationships. The greatly reduced basibranchial dentition of *Hypacanthus* (fig. 24a), suggests, however, that it did not share a common ancestor with *Parona-Scomberoides*.

Trachinotus, a circumtropical genus consisting of about 19 species (F. H. Berry, personal communication) that is at least superficially similar to *Hypacanthus*, differs from *Hypacanthus* and the other genera most notably in having dentary and premaxillary teeth that are poorly developed or absent; upper pharyngeals that are noticeably enlarged and covered with blunt, molariform teeth; the parasphenoid expanded into a broad, flattened plate posteriorly; and the basioccipital with a pair of lateral processes on its ventral surface. The complete absence of basibranchial dentition in *Trachinotus* represents the end product of a trend toward specialization in the opposite direction from that of *Parona-Scomberoides*. All of the above characters are probably correlated and constitute a single character complex associated with trophic ecology. Although the species of *Trachinotus* comprise a well defined group, there are no characters that are useful in establishing from what group of carangids they evolved.

Subfamilial Recognition.

In comparing the Carangidae to the Scombridae, Starks (1911) made the following observations which illustrate some of the problems encountered in subfamilial partitioning of the Carangidae: "The family Carangidae is a much more compact group than the Scombridae. The gaps between the genera are much smaller, and though the osteological characters, like the form of the body, differ much in the extremes of variation, there are no sudden or complete changes." Although he recognized four subfamilies (Scomberoidinae, Trachinotinae, Naucratinae, and Caranginae), Starks (1911, p. 30) acknowledged the largely artificial nature of these subfamilies by stating: "though *Selene* is not nearly so closely related to *Trachyurops* [= *Selar*]—for instance—as some forms are to each other that are here arranged in different subfamilies, there is no place to draw a dividing line." *Parona* and *Scomberoides* are probably no more divergent phylogenetically than are some genera presently placed together in the subfamily Caranginae. Within the present classification of the family, *Parona* might be recognized as a monotypic tribe in the subfamily Scomberoidinae. *Hypacanthus* would require its own subfamily, since its relationship to other carangid genera is obscure. Until the relationships of the other genera are better understood, we prefer not to recognize any carangid subfamilies.

The following characters shared, in combination, by *Oligoplites*, *Scomberoides*, *Parona*, *Trachinotus*, and *Hypacanthus* distinguish them as a group from all other carangids: lateral line without scutes; body moderately to strongly compressed; second dorsal-fin base approximately equal in length to anal-fin base; and haemal spine of first caudal vertebra and first anal pterygiophore firmly attached to form a strong strut. These characters may, however, have little or no phylogenetic significance. Other characters possessed by these five genera are summarized in table 7.

Phylogenetic Position of *Campogramma* Regan, 1903

(Figure 26)

Wheeler (1963) illustrated this poorly known eastern Atlantic-Mediterranean carangid and discussed its nomenclatural history. We agree with Wheeler (1963, p. 538) that the description of *Centronotus glaycos* Lacépède, 1803 is sufficiently diagnostic to determine its specific identity, thereby establishing it as a senior synonym of the widely used but nomenclaturally invalid name *Campogramma*

Table 7. *Summary of selected characters used to define genera.*

Character	*Trachinotus*[1]	*Hypacanthus*	*Parona*	*Scomberoides*	*Oligoplites*
epiotics united internally	no	no	yes	yes	yes
fronto-supraoccipital crest	high	low	high	low	low
suborbital shelf	present	present	present	present	absent
suborbitals 2–4 expanded posteriorly	no	no	no	no	yes
interosseous space between dentary and articular	well developed	moderate	well developed	minute	minute or absent
supramaxilla	absent	small	large	small	absent
premaxillary frenum	absent	absent	present (narrow)	present (wide)	present (wide)
dentary teeth	villiform band (often absent in adults)	wide band	narrow band (single row posteriorly)	2 rows	2 rows
'mesopterygoid' teeth	absent	absent	present (free-floating)	present (ankylosed to bone)	absent
branchiostegal rays	7–8	8	9	8	7
basibranchial tooth plates	absent	poorly developed	well developed (large median plate)	well developed (paired plates)	well developed (paired plates)
caudal vertebrae	14	14	17	16	16
inferior vertebral foramina	absent	present	absent	absent	absent
epural bones	3	3	3	2	2
predorsal bones	4 or 5 (rarely 5)	3	4	3 or 4 (rarely 4)	4 to 6 (rarely 4)
dorsal-fin rays	VI–VII+ I, 16–29	VII+ I, 19–21	VI–VII+ I, 32–38	VI–VII+ I, 19–21	IV–VI (rarely VI)+ I, 18–21
posterior dorsal- and anal-fin rays	normal	normal	normal	semidetached finlets	semidetached finlets
pelvic fins	present	present	absent	present	present
postpelvic processes	united distally	forming apical fork	united distally	united distally	united distally
postcoracoid process	moderate	moderate	well developed	absent	absent
first anal pterygiophore expanded antero-laterally, forming roof over anal spines	no	no	no (fig. 15a)	yes (fig. 15b)	yes like *Scomberoides*
body scales	oval-shaped	oval-shaped, becoming strongly lanceolate on breast	oval-shaped	broadly lanceolate to needlelike (fig. 3)	needlelike
cheek scales	present or absent	present	absent	absent	absent
lateral line	normal	irregular and sinuous dropping below midline of body between pelvics and anal fin	5–9 dorsal branches	normal	normal
swimbladder	simple (young) to moderately bifid (adults)	simple (young) to moderately bifid (adults)	simple (all sizes)	strongly bifid (all sizes)	strongly bifid (all sizes)

[1] Several unique characters of *Trachinotus* not included here are discussed in the text under Relationships and Zoogeography.

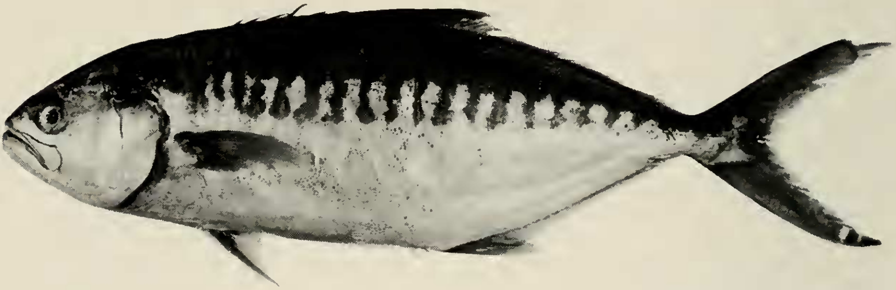

Figure 26. *Campogramma glaycos*, BMNH 1892.4.20.3, 377 mm. SL. Mediterranean. Snout appears unnaturally short due to bent condition of specimen.

vadigo (Risso, 1810). We do not agree with Wheeler who treated *C. glaycos* as a *nomen oblitum* because past workers either overlooked the name or considered it unavailable because of homonymy with *Lichia glauca* of authors. In fact, *C. glaycos* can not be considered a homonym of the differently spelled *L. glauca*. *Campogramma liro* proposed by Dollfus (1955, p. 58) as a replacement name for *C. vadigo* Risso is unnecessary. A junior synonym of *Campogramma glaycos* (Lacépède) overlooked by Wheeler is *Oligoplites africana* Delsman (1941). Bauchot and Blanc (1963, p. 53) proposed *Solagmedens* with *Oligoplites africana* as the type species. They apparently were unaware of the description of *Campogramma*.

Recent authors have assigned the monotypic *Campogramma* to the subfamily Trachinotinae, but without presenting substantiating data. Characters used to define the Trachinotinae that are associated with trophic ecology, such as enlarged pharyngeals and expansion of the parasphenoid posteriorly into a broad flattened plate, are absent in *Campogramma*. Three external characters of *Campogramma* that are shared, in combination, exclusively with naucratinine (= Seriolinae) genera are: lateral line without scutes; body terete, only slightly compressed; anal-fin base shorter than second dorsal-fin base.

The osteology of *Campogramma* suggests that it evolved from a form close to *Seriola*. The haemal spine of the first caudal vertebra is weakly articulated with the first anal pterygiophore, not enlarged and indistinguishable from the haemal spines of other caudal vertebrae. In lateral view the anterior margin of the first anal pterygiophore is distinctly concave, with a free distal tip, as in most species of *Seriola* (Mather, 1971, p. 186, fig. 3b). The last three pairs of parapophyses are connected dorsally by a bony bridge which encircles the haemal canal, and the last two are united distally to form a single haemal spine. As noted by Starks (1911, p. 29), in the other carangid subfamilies the posterior parapophyses are distinct, and not united as a single haemal spine, though a bony bridge connects their bases. Other characters shared with *Seriola* are:

zygapophyses of exoccipital joined beneath foramen magnum; myodome with a large posterior opening; large supramaxilla; premaxillary spur present; branchiostegal rays 3 + 4 (epihyal + ceratohyal); vertebrae 10 + 14 = 24; caudal skeleton with 3 epurals; cluster of free-floating, irregularly shaped patches of minute granular teeth overlying mesopterygoids; and swimbladder not bifid.

Campogramma is distinguished from all other genera of Naucratinae in having a single row of caniniform teeth in both jaws, naked cheeks, partially naked breast, and slightly falcate pectoral fins.

Material examined. BMNH 1893.2.24.3, 112 mm. SL, cleared and stained; BMNH 1892.4.20.3, 377 mm. SL, x-rayed.

Summary

The carangid fish genera *Scomberoides*, *Oligoplites*, *Parona*, and *Hypacanthus* are revised. These four genera, along with *Trachinotus*, are distinguishable as a group from all other genera of Carangidae. *Campogramma*, formerly placed in the subfamily Trachinotinae, is considered to be more closely related to *Seriola*.

Scomberoides consists of four recent species, *S. commersonianus* Lacépède, *S. tala* (Cuvier), *S. lysan* (Forskål), and *S. tol* (Cuvier). *Scomberoides spinosus* (Smirnov), described from Lower Miocene deposits, is believed to be closely related to *S. tol*. *Scomberoides lysan*, consistently treated as a senior synonym of *S. commersonianus*, is instead a senior synonym of the widely used *S. tolooparah* (Rüppell). The species of *Scomberoides* range from the Indian Ocean and Red Sea into the central Pacific; only one species, *S. lysan*, occurs east of the Solomon Islands and frequents entirely oceanic habitats.

Oligoplites consists of five species, *O. saurus* (Bloch and Schneider), *O. saliens* (Bloch), *O. palometa* (Cuvier), *O. refulgens* Gilbert and Starks, and *O. altus* (Günther). *Oligoplites mundus* Jordan and Starks is placed in the synonymy of *O. altus*. The genus is restricted to the eastern Pacific and western Atlantic oceans; only *O. saurus* occurs in both oceans.

Parona, a monotypic genus restricted to the western South Atlantic Ocean, is believed to be most closely related to *Scomberoides* and *Oligoplites*. *Parona signata* (Jenyns) is unique among carangids in that it lacks pelvic fins.

Hypacanthus, also monotypic, has a littoral distribution in the Mediterranean Sea, along the Atlantic coast of Africa, and the southern Indian Ocean. *Hypacanthus amia* (Linnaeus) is the least specialized of the carangids studied.

Osteological descriptions are given for *Scomberoides*, *Oligoplites*, *Parona*, and *Hypacanthus*. Of the genera treated, *Scomberoides* and *Oligoplites* are the most closely related, with *Oligoplites* the most specialized. Within the framework of the present classification of the family Carangidae the two monotypic genera would require their own subfamilies. The phyletic relationship of all of these genera is such that we do not recognize any subfamilies.

Appendix

List of Nominal Species of *Scomberoides* and *Oligoplites*, Including Some Names Originally Assigned to One of These Genera (or Their Synonyms) That Were Misapplied or Are Unidentifiable.

The following list gives in order: (1) the scientific name in alphabetical order by species as it originally appeared (capitalized specific names in lower case, however); (2) the author or authors (Cuvier and Valenciennes, 1831 is abbreviated to C. & V., 1831, and Jordan and Evermann, 1898 is abbreviated to J. & E. 1898); (3) date of publication; (4) page reference (see literature cited section for complete reference); the genus and species to which we currently assign the species, if such is possible. Included are several nominal species described in *Scomberoides* or *Chorinemus* that are unidentifiable. The basis for our assignment of nominal species of *Scomberoides* is discussed in the text under their senior synonyms. Unless stated otherwise in the text, synonymy of *Oligoplites* species follows that of Schultz (1945).

Species, author, publication date, and page reference	Present allocation
Oligoplites africana Delsman, 1941, p. 52	*Campogramma glaycos*
Lichia albacora Guichenot, 1848, p. 231	*?Oligoplites altus*
Chorinemus altus Günther, 1868, p. 433	*Oligoplites altus*
Scomber calcar Bloch, 1793, p. 46	*?Oligoplites saliens*
Scomberoides commersonnianus Lacépède, 1802, p. 50	*Scomberoides commersonianus*
Chorinemus delicatulus Richardson, 1846, p. 269	*Scomberoides commersonianus*
Chorinemus exoletus Ehrenberg *in* C. & V., 1831, p. 379 (278)	*Scomberoides commersonianus*
Chorinemus farkharrii Cuvier *in* C. & V., 1831, p. 388 (285)	unidentifiable (?Scombridae)
Scomberoides formosanus Wakiya, 1924, p. 236	*Scomberoides tol*
Scomberoides formosanus Oshima [non Wakiya], 1925, p. 349	*Scomberoides lysan*
Scomber forsteri Bloch & Schneider, 1801, p. 26	*Scomberoides lysan*
Chorinemus guaribira Cuvier *in* C. & V., 1831, p. 393 (289)	*Oligoplites palometa*
Chorinemus hainanensis Chu and Cheng, 1958, p. 317	*Scomberoides tala*
Oligoplites inornatus Gill, 1863, p. 166	*Oligoplites saurus inornatus*

Chorinemus lanceolatus Girard, 1858, p. 168	*Oligoplites s. saurus*
Chorinemus leucopthalmus Richardson, 1846, p. 269	*Scomberoides commersonianus*
Scomber lysan Forskål, 1775, p. 54	*Scomberoides lysan*
Scomber maculatus Forster, 1844, p. 195	*Scomberoides lysan*
Chorinemus maculosus Saville-Kent, 1893, p. 369	*nomen nudum* (*Scomberoides* species)
Scomber madagascariensis Shaw, 1803, p. 590	*Scomberoides commersonianus*
Chorinemus mauritianus Cuvier *in* C. & V., 1831, p. 382 (281)	*Scomberoides lysan*
Chorinemus moadetta Ehrenberg *in* C. & V., 1831, p. 382 (280)	*Scomberoides lysan*
Thynnus moluccensis Gronovius *in* Gray, 1854, p. 121	*Scomberoides lysan*
Oligoplites mundus Jordan & Starks *in* J. & E., 1898, p. 2844	*Oligoplites altus*
Scomberoides noelii Lacépède, 1802, p. 50	unidentifiable (?Scombridae)
Chorinemus occidentalis Günther, 1860, p. 475	*Oligoplites s. saurus*
Chorinemus orientalis Temminck & Schlegel, 1844, p. 106	*Scomberoides lysan*
Scomberoides oshimae Whitley, 1951, p. 65	*Scomberoides lysan*
Chorinemus palometa Cuvier *in* C. & V., 1831, p. 392 (288)	*Oligoplites palometa*
Eleria philippina Jordan & Seale, 1905, p. 744	*Scomberoides tala*
Lichia quiebra Quoy & Gaimard, 1824, p. 365	*Oligoplites* (*?s. saurus*)
Oligoplites rathbuni Miranda-Riberio, 1915, p. 8	*Oligoplites s. saurus*
Oligoplites refulgens Gilbert & Starks, 1904, p. 73	*Oligoplites refulgens*
Scomber saliens Bloch, 1793, p. 41	*Oligoplites saliens*
Chorinemus saltans Cuvier *in* C. & V., 1831, p. 393 (289)	*Oligoplites s. saurus*
Scomberoides saltator Lacépède, 1802, p. 50	*Oligoplites saliens*
Chorinemus sancti petri Cuvier *in* C. & V., 1831, p. 379 (279)	*Scomberoides lysan*
Scomber saurus Bloch & Schneider, 1801, p. 32	*Oligoplites s. saurus*

Palaeoscomber spinosus Smirnov, 1936, p. 49–59	*Scomberoides spinosus*
Chorinemus tala Cuvier *in* C. & V., 1831, p. 377 (277)	*Scomberoides tala*
Chorinemus tol Cuvier *in* C. & V., 1831, p. 385 (283)	*Scomberoides tol*
Chorinemus toloo Cuvier *in* C. & V., 1831, p. 377 (277)	*Scomberoides* (?*tala*)
Lichia tolooparah Rüppell, 1828, p. 91	*Scomberoides lysan*

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